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DEPARTMENT OF MARINE BIOLOGY
OF
CARNEGIE INSTITUTION OF WASHINGTON
ALFRED G. MAYER, DIRECTOR

PAPERS FROM THE TORTUGAS LABORATORY

OF THE

CARNEGIE INSTITUTION OF WASHINGTON

VOLUME II

WASHINGTON, D. C.
PUBLISHED BY THE CARNEGIE INSTITUTION OF WASHINGTON
1908

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CARNEGIE INSTITUTION OF WASHINGTON

PUBLICATION NO. 103

PRESS OF
THE NEW ERA PRINTING COMPANY
LANCASTER, PA.

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I. HABITS, REACTIONS, AND ASSOCIATIONS IN OCYPODA ARENARIA.
By R. P. COWLES.

II. HABITS, REACTIONS, AND MATING INSTINCTS OF THE WALKING-STICK, APLOPUS MAYERI.
By CHARLES R. STOCKARD.

III. STUDIES OF TISSUE GROWTH: I. AN EXPERIMENTAL STUDY OF THE RATE OF REGENERATION IN CASSIOPEA XAMACHANA.
By CHARLES R. STOCKARD.

IV. SOME INTERNAL FACTORS CONCERNED WITH THE REGENERATION OF THE CHELÆ OF THE GULF-WEED CRAB.
By CHARLES ZELENY.

V. A CONTRIBUTION TO THE LIFE-HISTORIES OF THE BOOBY AND MAN-O'-WAR BIRD.
By F. M. CHAPMAN.

VI. THE HABITS AND EARLY DEVELOPMENT OF LINERGES MERCURIUS.
By E. G. CONKLIN.

VII. TWO PECULIAR ACTINIAN LARVÆ FROM TORTUGAS, FLORIDA.
By E. G. CONKLIN.

VIII. THE BEHAVIOR OF NODDY AND SOOTY TERNS.
By J. B. WATSON.

IX. AN EXPERIMENTAL FIELD-STUDY OF WARNING COLORATION IN CORAL-REEF FISHES.
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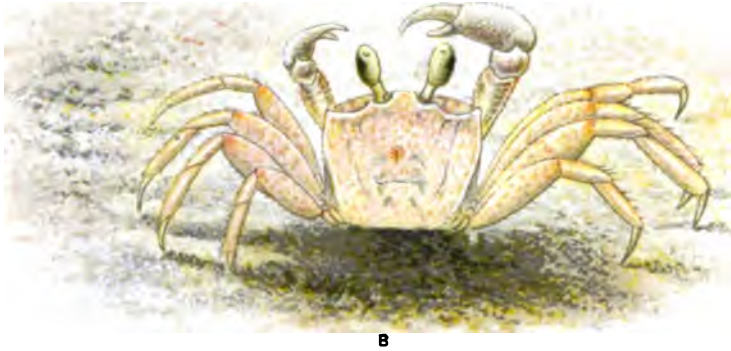

B

C

C. Kellner.

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I. HABITS, REACTIONS, AND ASSOCIATIONS IN OCYPODA ARENARIA.

BY R. P. COWLES,

Instructor in Biology in Johns Hopkins University.

4 plates and 10 text figures.

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HABITS, REACTIONS, AND ASSOCIATIONS IN OCYPODA ARENARIA.[1]

By R. P. Cowles.

One of the most interesting crustaceans that inhabits the Atlantic Coast of the more southern States is the brachyuran *Ocypoda arenaria,* the so-called " sand-crab," and no one who sees this lively creature can help marveling at the rapidity and dexterity of its movements as it scampers over the beach sands. While the adult has not been reported north of New Jersey, Verrill (1874) tells us young specimens have been seen by Mr. S. I. Smith at Fire Island, Long Island, by himself at Block Island, Rhode Island, and that the *megalops* larva has been taken in abundance by Mr. Vinal Edwards in Vineyard Sound. Verrill has suggested that ocypodas found in the Northern States are carried there from the South by the Gulf Stream while in the larval condition and that each winter they are killed off by the cold weather, so that they never grow large enough to breed. This supposition seems to be very plausible, since none but half-grown specimens are found in those regions and since breeding occurs in the South at just about the right time to make it possible for larvæ to be carried up in the early spring. The adult has been reported from Cobb Island, Virginia, and it is very common along the sea-beach in the region of North Carolina. It flourishes in the Bahamas, on the sandy keys of Florida, and is found as far south as the coast of Brazil.

During the summers of 1905 and 1906 it was my good fortune to spend a few weeks in the Marine Biological Laboratory of the Carnegie Institution of Washington at Loggerhead Key, Florida. On this key specimens of *Ocypoda arenaria* were very abundant, and owing to the small size of the island it was an easy matter to study them at all times of the day while only a short distance from the laboratory. A preliminary report of my observations during the summer of 1905 has been published in the Year Book of the Carnegie Institution of Washington, No. 4, 1905.

My purpose in studying *Ocypoda* was to learn as much as possible concerning its behavior and to determine how far it was able to form associa-

[1] I wish to express my thanks to the Carnegie Institution of Washington and to Dr. A. G. Mayer, Director of the Marine Laboratory at Tortugas, for many courtesies extended to me.

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tions. I found a quantitative investigation of this latter point very difficult, owing to the inhibition of normal behavior under artificial conditions, but several experiments showed conclusively that they formed associations.

METHODS.

Much care was taken, while observing the behavior of ocypodas and while experimenting with them, to have the conditions as favorable as possible. For the observation of their normal behavior in nature a white tent was used for a time to conceal the observer, but it was found that this was unnecessary and that they could be studied equally as well from the window of a well-ventilated building built out partly over the water some distance from the laboratory proper. From this window, with the aid of a good pair of bird-glasses, many interesting points in the behavior could be distinctly seen without in any way disturbing the crabs.

The best time of day for watching the ocypodas seemed to be from sun-up until about 11 a. m. and from 5 to 6 p. m. During the middle of the day the adults were usually down in their burrows, but there were often a few of the younger ones out at this time. Individuals were also observed during the night, when one might approach quite closely to them without interrupting their feeding.

A simple trap for collecting ocypodas to be used in experiments was made in the following manner: A deep hole was dug in the sand above the high-tide mark and in it was placed a large dry-goods box without a cover. It was so placed that the open end was flush with the surface of the sand and boards several inches wide were nailed horizontally around the upper edge so as to prevent the crabs from climbing out. On one occasion during the first night 3 individuals were caught; on the next night the number was increased to 6; on the next to 12, and on the next to 24. While in this special case food and water were kept in the trap, it was found at other times that the trap was equally as effective when nothing of this sort was present. Whether the ocypodas dropped into the trap by accident or whether they were attracted there I am unable to say.

BURROWS.

As is well known, *Ocypoda* lives in burrows which it digs in the sand along the seashore. At Loggerhead Key the large majority of the burrows are found on the sloping beach all around the island, extending from the shore-line to 20 or 30 feet from it, but quite often stray ones occur in the interior of the island many feet from the water's edge. During my stay at Loggerhead Key I found several ocypodas living close to the steps of the laboratory, probably for the purpose of picking up stray pieces of refuse which might be thrown from the doors of the station. Around the kitchen, which is situated over the water's edge, the habitations of the crabs were

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very numerous, and at certain times of the day large numbers could be seen moving around near it in search of food.

Ocypoda usually makes its burrows on the sloping beach; in some cases, however, they occur on perfectly level ground, and in others, where the beach has been washed away, they are found dug into the vertical surface of the shore. There are three kinds of burrows, all very simple. One consists of a tunnel which is not perfectly straight, extending down into the sand at an angle of about 45° with the surface. This tunnel opens to the exterior at one end, terminates blindly at the other, and has a more or less vertical passage branching off from it and sometimes communicating with the exterior by an opening (see fig. 1). The opening of the vertical passage is

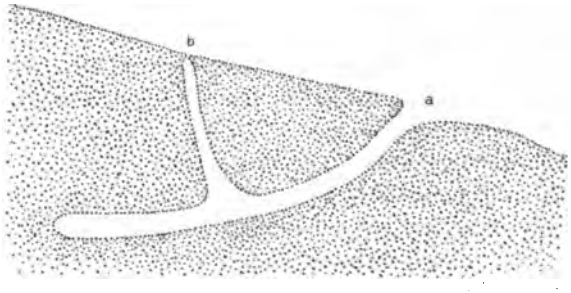

FIG. 1.—Longitudinal vertical section through a burrow with two openings. *a*, entrance; *b*, opening for escape.

always farther away from the water-line than the main tunnel. As a rule these burrows extend directly away from the shore-line, but sometimes they do not exactly. The depth varies considerably, averaging 1 or 2 feet. Another kind of burrow, which occurs higher up on the beach, is like those just mentioned except that it is much deeper and does not have any branching passage. One of these, when carefully followed to its end, was found to extend 4 feet 2.5 inches, ending in coarse, wet sand. It occurred to me that these deep burrows might be used by the females during the breeding season and also that they might be used for molting purposes, but I have no observations to support the truth of these statements. As a matter of fact I have never found females with eggs at the bottom of their burrows, nor have I found casts. It is also true, however, that I have never found the casts on the surface of the ground.

Very young ocypodas make still another kind of burrow which extends vertically downward into the wet sand for only a few inches.

The burrow first described is much more numerous than any other kind and is more interesting on account of the branching passageway connected with it. I have examined many of these burrows in the effort to find the use of the branch. As stated above, sometimes the passage opens to the

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exterior and sometimes it does not. In the first case I have found it used only rarely for entrance and exit. As a rule the opening of the branch passage is much smaller than that of the burrow proper and usually there are no tracks leading from the opening of the branch passage, while the sand around the entrance to the burrow is covered with them. These facts seem to indicate that the branch passage is not made for habitual entrance and exit.

It occurred to me that this second opening might be a means of ventilating the burrow, thus making it cooler. There are absolutely no facts to support this theory, especially since it is found that the deep burrows, which would need ventilation if any did, were without these branching passages.

Some light was thrown on the question when an ocypoda was observed digging its burrow. After it had dug for a certain distance, bringing up the sand at regular intervals, it remained down in the burrow for some little time and then suddenly there occurred a disturbance of the surface of sand in about the region where the opening to the second passageway should be. The sand began to sink in a little, but no opening was formed, and it remained in this condition until I dug up the burrow, when it was found that the crab had made a branch passage, starting from the burrow and working up almost to the surface without quite breaking through. Such a procedure was witnessed on more than one occasion, and each time the branch passage did not quite break through to the surface.

After observing this it occurred to me that the passage might be used in time of need to escape from enemies, and I soon witnessed a sight which convinced me that such was the case. One ocypoda was in possession of a burrow with a branching passage, when another appeared at the opening of the burrow. The owner immediately went down and the intruder followed for a short distance and then returned to the opening, followed by the owner. This was repeated several times, the intruder going down farther each time, when suddenly the owner climbed up into the branching passage, broke through the surface and scampered away, leaving the intruder in possession. The two crabs were evidently contending for the possession of the burrow, and it seems probable that when the owner was unable to keep the intruder out it escaped by the only means possible in order to prevent injury to itself when driven to the end of the burrow.

This same procedure was witnessed several times, but occasionally it was varied by the owner going around to the opening of the burrow and driving the intruder up through the branching passage instead of running away after its escape. Frequently this chase in through the burrow opening and out through the branched passage would be continued for some time, making a very ludicrous sight for the observer.

The behavior just mentioned, together with the facts that the opening of the branching passage is usually not made at the same time the passage is, and that there are but few, if any, tracks around the opening, leads me to

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believe that it is used for escape by the ocypodas when they are hard pressed. It seems most remarkable that these crabs should often dig the escape passage out almost to the surface without breaking through, thus leaving the place of exit concealed.

While the above description of the burrows applies to the large majority, there is considerable individual variation to be seen both in the construction of the burrow and the manner of doing the work. Some have arched roofs with an almost level floor, and others are almost round in cross-section. While, as has been described, the burrow usually points directly away from the water, there are some that extend obliquely, and in one or two cases burrows have been found which lead toward the water. Some individuals, especially the older ones, finish these burrows carefully, while others do not; some work quickly and others slowly; some start many burrows, but finish none; and many drive individuals out of the burrows they have made and take possession.

As would be expected, *Ocypoda* usually digs its burrow in a place where the sand is firm and damp below the surface. It scratches out a shallow hole with its walking appendages, making it deeper and deeper, until it is unable to simply scratch the sand away, when it begins to carry it out in the following manner (plate 2, fig. A): Using the first and second walking appendages and chelæ of one side, it rakes up quite a good-sized load, holding it firmly between the appendages and the body proper. It then crawls out of the hole and deposits the sand, sometimes throwing it by a quick movement of the chelæ and walking appendages for a distance of almost a foot, sometimes carrying it away 2 feet or more and depositing it quietly, and occasionally dropping it immediately in front of the mouth of the burrow.

As is well known, *Ocypoda* has one chela decidedly larger than the other, and in nearly every case in which an individual was observed making its burrow it went down into the tunnel sideways with the side having the small chela foremost, using that side in the digging and carrying of the sand (fig. 2). Out of 17 cases in which ocypodas were observed going down into their holes, after the burrow was constructed, the side with the small claw led the way 16 times. The small-chela side is undoubtedly better adapted for digging, which may account for this phenomenon. Furthermore, under these conditions the crab is better protected from any enemy which may come down after it, since its large fighting chela is presented to the intruder.

On some occasions I have noticed individuals lying on their backs in the tunnels digging away at the roof, and this is probably the manner in which the vertical passage is started.

Many ocypodas exhibit considerable care in the construction of their burrows, especially the entrance to them. Sometimes, when the approach to the opening is quite steep, the crab will pile the sand that it brings from the

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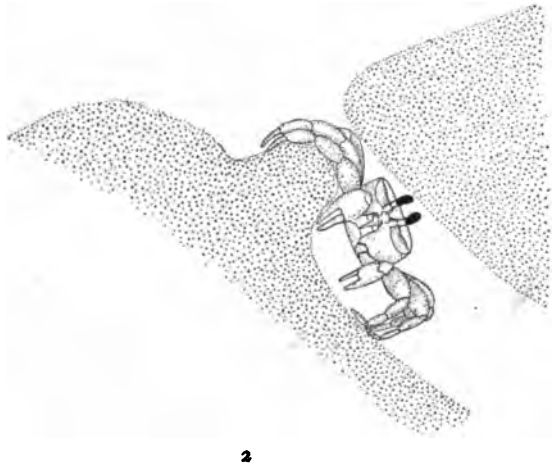
burrow in front of the opening and then very carefully tamp it down, using the broad surface of its large chela and the distal segments of the walking legs. Sometimes, if there is a small hollow in the surface, it will drag sand from another place into the hollow and press it down. Often an ocypoda will carefully tamp the sand that it has thrown away, for a radius of over a foot, and frequently it will smooth off the edges of the opening into the burrow. Almost invariably, unless startled, before an individual goes down into a burrow, either while constructing it or after, it will halt for some little time, apparently surveying the region around to see if there are any intruders about.

A most interesting performance that I have frequently observed is the closing of the burrow. This usually occurs after the crab has stocked it with food. Upon several occasions I have thrown a number of small fish to an individual, each one of which was carried down and deposited at the blind end of the tunnel. Then the crab would gather up a load of sand from out-



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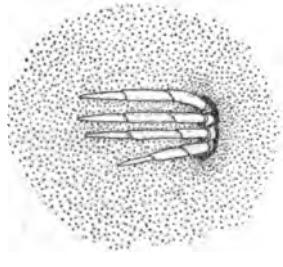

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FIG. 2.—Diagrammatic longitudinal section through burrow which an *Ocypoda* is plugging up.

FIG. 3.—View of plug from above, showing ambulatory appendages tamping surface of plug; mouth reduced to small hole.

side the burrow, draw it into the entrance, pressing it firmly on one side of the opening (fig. 2). After this it would come out of the half-closed entrance, take up another load of sand, return and enter, drawing the sand after it. This load would be placed alongside of the other and would practically close up the entrance, leaving, however, the distal joints of several of the walking legs outside. With these the ocypoda would carefully tamp down the plug now formed and finally quickly draw them in, leaving sometimes only a very small hole and sometimes none at all (fig. 3). By this means the entrance to the burrow was very effectually concealed.

Sometimes, when individuals are disturbed by other crabs or by man, they

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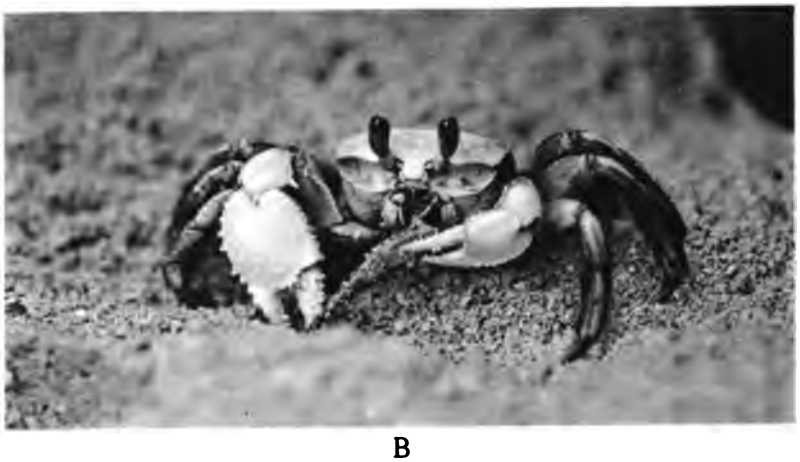

B

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A. Ocypoda carrying sand from burrow.

B. Ocypoda feeding.

C. Defensive attitude "Aufbäum" reflex.
½ natural size.

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will run into their burrows for a few inches and push a plug of sand up from below, completely closing the entrance.

It seems probable that not more than one ocypoda at a time makes a burrow its home, unless during the breeding season, although I have seen as many as three emerge from a single hole. Most of the burrows are not permanent living-places, since they are usually made below high tide. Individuals often drive one another out of their burrows, and the successful one usually appropriates the new home that it has won; on several occasions three in succession have been seen to gain possession of the same burrow.

BREEDING SEASON.

The breeding season of *Ocypoda* was practically at an end when I visited Tortugas in June, but my own observations and those of others lead me to believe that it occurs probably in the spring and early summer rather than throughout the summer, as suggested in my preliminary report. During the late summer of 1906 I examined many female specimens, but only in a few cases did I find any eggs, and these were always few in number, suggesting the last of a brood. Mr. Kellner, who was at Tortugas as early as March, states that at that time large ocypodas were quite scarce, but that very little ones were quite numerous. Later, however, according to his observations, the adults began to appear again, so that in June they were present in considerable numbers. It seems very probable that farther north along the Atlantic Coast the breeding season is somewhat later.

There is scarcely any difference in appearance between the male and female ocypodas, except in the shape of the abdominal segments (plate 3) and the abdominal appendages. The females, however, are usually clean-looking and less scarred than the males. Both have the stridulating ridge, of which I shall have something to say later (page 28).

During the time that I was at Loggerhead Key the males seemed to be much more in evidence than the females. In nearly every case when burrows were dug up and individuals were found inside they were males. The traps also always showed a larger number of males than females.

FOOD AND FEEDING.

Ocypoda is often found feeding during the daytime, but more especially at night (plate 2, fig. B). It is also a cannibal, and to test this characteristic a small trap was stocked with many small individuals measuring from 1 to 2 cm. across the carapace. During the night two larger individuals, about 4 cm. across the carapace, dropped into the trap and in the morning most of the small ones were found torn to pieces, with the soft parts eaten out. It is interesting to note that when a trap is set only large individuals are found as a rule in the morning. In a trap which had caught 30 ocypodas during several nights no small ones were found, and it seems probable that they

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do not enter on account of the presence of the adults. If they drop in by chance they are almost always killed and eaten. Among the many different kinds of food that *Ocypoda* will eat are cocoanut, sea-weed, bread, turtle-meat, fish, coffee-grounds, potatoes, ham fat, and jelly-fish. Bebe, in his article on "Birds of Cobb Island," states that the sand-crab eats bird's eggs, and Verrill (1874) has found that it feeds upon *Talochestia longicornis* and *T. megalophthalma*. When the dead body of a fish which has been washed ashore is too large to be carried away by an ocypoda, it is apt to build a burrow by the side of the fish and feed on it day after day. Dr. Mayer has observed that when *Physalia* are driven up on the beach the same thing occurs, and then there is usually only one burrow to each *Physalia*.

Ocypodas are great scavengers and keep the beach almost free from decomposing animal and vegetable matter, but there are a few things that they will not eat; one of these is the lime. Pieces of this acid fruit thrown to them are seized immediately, but one "taste" seems to be sufficient. They immediately begin to rub the lime in the sand, apparently trying to get rid of a substance that irritates the sensory organs of the mouth. There is no doubt that this crab reacts more strongly to certain kinds of foods than to others.

While feeding ocypodas usually congregate along the drift-line of the beach, but as far as I have observed they never enter the water for the purpose of seizing food.

During the summer large schools of *Atherina laticeps* (sardine of the Gulf) are almost always found close to the shore of Loggerhead Key and they are an important food for *Ocypoda* (plate 2, fig. B). These small fish were frequently used in feeding experiments. Feeding was observed both while individuals were in captivity and while they were under natural conditions. The eyes do not seem to play an important part in the detection of food, although they undoubtedly serve to lead the crabs to objects which may be food. When atherinas are thrown near an ocypoda (the observer being concealed), the "sand-crab" usually jumps and runs toward the former as though it "knew" the fish were food, but, as we shall see from other experiments, this is probably not the case. As soon as the fish is reached the *Ocypoda* touches it with the claws and then immediately grabs it. As a rule the *Atherina* is carried at once into a burrow, but often (especially in case of the first few specimens) it is pinched with the claws, which are then rubbed against the first pair of maxilla situated at the mouth opening. Usually this process is repeated several times, alternating one claw with the other, until finally the crab has succeeded in introducing some of the juice into the mouth. Then it may hold the fish in one claw, using the other to tear off pieces and to transfer them to the mouth-parts, or it may grab the fish with either end directed toward the mouth, gnawing on it with the mouth-parts Frequently the *Ocypoda* begins by picking out the eyes of the *Atherina* and eating them.

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Whether one calls it taste or chemical sense, there is no doubt that *Ocypoda* is able to distinguish between foods. When several different kinds of food are presented to a number of individuals, certain kinds will be eaten in preference to others.

A rather interesting experiment was one where the feeding was observed in the case of an individual from which the small chela had been cut off close to the body. This specimen seemed to have great difficulty in adjusting a fish so that it could be eaten. An attempt was made to use the first ambulatory appendage on the side from which the chela had been removed, but the crab was not very successful in this, and after many trials it hit upon the following method: The fish was grasped about in the middle with the large chela in such a manner that the end was directed toward the mouth, and in this position feeding was accomplished with some difficulty. It would push the end of the atherina up against the mouth-parts, where the mandibles would take hold and then pull the fish away, thus tearing off pieces which could be eaten. This was repeated many times on different occasions.

Occasionally the "sand-crab" did not seem to be able to adjust the fish according to this method, and then holding the atherina with its one chela tightly against the sand, it tipped the body downward until the mouth-parts were in contact with the fish, when it proceeded to feed as usual.

"OLFACTORY ORGANS."

Nagel (1894) and Bethe (1895, 1897) have studied the crustacean *Carcinus mœnas* in the endeavor to find out in how far this crab makes use of the senses of smell and taste, or, as these have been called together, the "chemical sense." Both of these investigators have concluded that *Carcinus* in its search for food is aided by the chemical sense, and Bethe has gone so far as to say that the chemical stimuli are the principal ones that lead the crab to food, the eyes aiding only slightly or none at all. The experiments devised and the observations made, as recorded below, were for the purpose of determining if *Ocypoda* would react to foods at a distance through other senses than that of sight.

The so-called "olfactory organs" of *Ocypoda* are situated on the antennæ, which are very much reduced in size (plate 4, fig. c). They consist of the typical "olfactory hairs," which are open at the distal end and which have a nerve running part way up the axis. These hairs are not as numerous as the feathered tactile hairs which occur in a large bunch on the segment next to the basal segment of the antenna.

Dr. Mayer observed that ocypodas dug up decomposing fish which had been placed about the roots of young pineapple-plants, but this does not prove that the odor attracted them, for it is quite probable that the juices or small particles of the fish were left on the surface of the sand and that the ocypodas in their wanderings and search for food happened to pass over these places.

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Several experiments were devised to determine if *Ocypoda* would react to odors, and although the results were not conclusive they were of some interest.

Experiment 1.—Pieces of coral and small fish (*Atherina*) were dropped alternately near a crab. They ran for each and often carried the coral as well as the fish away with them. Precaution was not taken, however, to have the pieces of coral free from the odor of fish.

Experiment 2.—Atherinas soaked in carbon disulphide were thrown to the crabs and these were at once seized in all cases and carried into the burrows. As far as could be observed this ill-smelling liquid had no effect on the ocypodas.

Experiment 3.—Poured aqua ammonia down a burrow containing a crab. This burrow had two openings and a strong odor of ammonia came up through the second opening, showing that it penetrated through the entire burrow. This did not cause the crab to come out of its burrow until 10 minutes at least had passed, when it came out unaffected, as far as could be observed.

Experiment 4.—An atherina was wrapped in several thicknesses of newspaper, the ends being left open and care taken not to get fish juice on the newspaper. (The paper extended an inch beyond the fish at both ends.) This was then wrapped in Swiss book, tied at the middle, and dropped near the opening of a burrow. The crab soon came out, pinched it, and attempted to bite it at the open end. It seemed to react as it would toward an unconcealed fish, and it is not probable that the juices of the fish came in contact with the mouth-parts. Finally the package was taken down into the burrow, which was then closed up.

The same experiment was repeated, substituting a roll of newspaper for the fish and wrapping with Swiss book as in the former case. This package was then dropped and was almost at once grabbed and pinched, but soon left as though there were nothing attractive about it.

Experiment 5.—In this experiment a bowl-like hole was dug and atherinas were put in the bottom of it. They were then covered over with a layer of sand about an inch thick, so that they could not be seen, but so that the odor could be detected by the experimenter. A screen made of ¼-inch-mesh wire was then put over the excavation, so that the crabs could not reach the fish without digging under. Great care was taken not to allow the juices of the fish to get on the screen or the sand surrounding it. At the expiration of 10 hours the ocypodas had not made an attempt to dig down to the fish. There were many tracks on the sand, however, showing that the crabs had been examining the region. A crab was observed crawling over the screen, pinching the wires of the same and then rubbing its chela over the mouth-parts, which behavior is typical of the feeding reaction. This was repeated by the same crab, and seems to afford strong indications that *Ocypoda* may react to food at a distance through some other sense than those of sight or contact (figs. 4 and 5).

Experiment 6.—A young ocypoda which had not been fed for a day was used in this experiment. The eyes were painted with a mixture of shellac and lampblack, so that they did not react to shadows or to the movements of the hand near it. A fresh atherina was held within about 2 or 3 mm. from the mouth-parts for about 3 minutes. So far as could be seen the crab did

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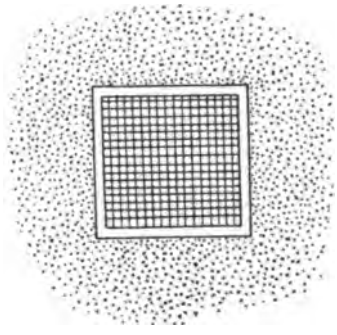
not react. There was no movement of the antennæ, such as Bethe (1895, 1897) has observed when a piece of meat is held near the mouth-parts, but when the fish was touched against one of the chelæ the ocypoda immediately jumped at it, took hold, pinched it, and put its chela up against its mouth-parts, after which it began to eat. There is nothing in the behavior of the crab in this experiment which proves that *Ocypoda* reacts to odors. However, the rapidity with which it determined that the object was food after the chela was touched leads me to believe that it had been stimulated by the odor of the fish before the chela was touched and that it inhibited the reaction on account of the abnormal conditions to which it was subjected. It is true that the fleshy consistency of the fish may have been a food-determining factor.

4



5

Figures illustrating experiment 5. Fig. 4, vertical section; fig. 5, seen from above.

In the following experiments an attempt was made to find out from how great a distance *Ocypoda* would react to food. A square 9.5 inches by 9.5 inches, divided up into 64 smaller and equal squares, was marked out on the sloping beach in a region where it could be seen by the experimenter while he was practically concealed about 10 feet above the sand in a house nearby. Small pieces of decomposing fish about 1.5 c.cm. in volume, fragments of coral, and pieces of black glass were used to attract the crabs.

Experiment A.—A piece of fish was placed at the center of the square, as shown in fig. 6. An ocypoda came to point A_1 and began to make a burrow. After a few digs it went straight for the center of the square (A_2) and grabbed the fish with no hesitation. The wind was blowing in the direction shown[1] and the meat was on the surface of the ground. An important condition in this experiment, as we shall see in another section, was that flies were moving about on the meat and frequently flying to and away from it.

Experiment B.—The conditions in this experiment were the same as in Experiment A and the results were the same except that the crab stopped at B_2 for 2 or 3 seconds while on its way to the meat.

While the crab in these two experiments may have reacted to the odor of the fish, the eyes undoubtedly received a stimulus that determined the movement toward the food.

Experiment C.—A piece of fish meat was placed in the center of the square. A crab 2.5 feet from the center (C_1) went directly to the meat

[1] In experiments A to J the wind was blowing across the square from the upper left-hand corner to the lower right-hand corner.

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(C_2), returned to C_2 and went down into its burrow. A brisk wind was blowing directly away from the crab and there is no doubt that the latter did not react to the odor of the fish.

Experiment D.—In this experiment a piece of black glass 2 cm. wide and 4 cm. long was stuck in the sand at the center of the square. A crab at D_1, facing away from the center of the square, moved slowly but straight for the black glass. To my surprise it went backward all the way, striking the glass squarely in the middle of the posterior side of the carapace. Later it was found that this was not an unusual way for a crab to approach an object. After digging around the piece of glass and pinching it several times it was abandoned. Here odor could not have been a factor in the behavior of the crab nor could the movement of flies, for there were none present.

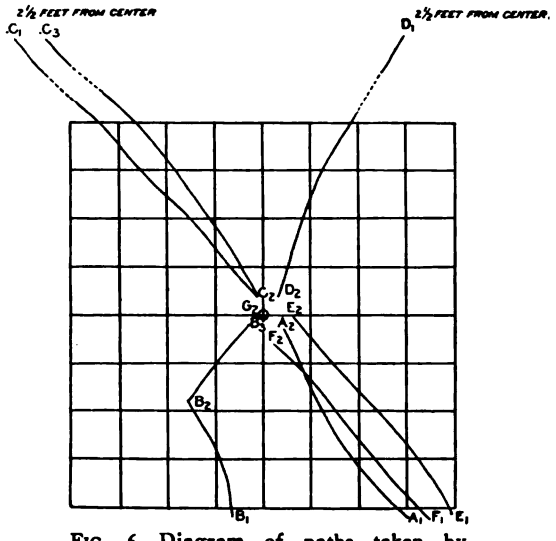

FIG. 6—Diagram of paths taken by ocypodas in experiments A to F.

Experiment E.—A piece of white coral about 2 by 4 cm. was placed at the center of the square. A crab whose burrow was at E_1 came out, but showed very little inclination to examine the coral. It was almost 5 minutes before it started for the coral and then it moved slowly. As in the case of experiment D, flies were not present.

Experiment F.—Several pieces of white coral smeared with the juices of decomposing fish were placed at the center of the square. The subject of the experiment in experiment E did not move toward the coral at once, but as flies began to alight the crab approached and attempted to get something to eat off of it. Soon, however, it returned to its burrow. The flies which had been driven off by the attack of the crab then came back and with their return the crab quickly approached the center of the square. Instead of leisurely taking hold and pinching the coral it gave a little jump in the seizure, as it does in the case of a live fish. The flies were driven away, after which the ocypoda returned to its burrow. This performance was repeated fifteen or twenty times, approaching, jumping, seizing and returning, after which the coral was abandoned, the crab apparently paying no more attention (objectively speaking) to it nor to the flies collected upon it. The ocypoda then began to dig its burrow, and when other individuals came and attempted to eat from the coral it did not chase them away, but merely stood guard at the entrance to its home.

The eyes in this experiment played the most important part in the behavior of the crab, and there is no doubt that *Ocypoda* associates the presence of flies, or rather the difference in the intensity of light resulting from the movement of the flies, with the presence of food. Its behavior can

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hardly be explained in any other way, and, as we shall see below, the movement of objects has an important influence on the behavior of *Ocypoda.*

Experiment H.—A piece of decomposing fish was placed in a hole at the center of the square, the hole was filled up and the surface then smoothed off. The observer then left, but after 30 minutes returned and found that a crab had dug the fish out and carried it away. Considerable precaution was taken to prevent the surface sand from touching the fish or its juices, so that the indications are that the ocypoda found the food through the stimulus of odor, the eyes not aiding in its detection.

Experiment I.—In this experiment a piece of decomposing fish was fastened to the end of a stick, which was then stuck in the sand, so that the meat was 60 cm. from the ground. A crab ran up to the stick, pinched it, and tried to reach higher than usual with its chelæ, but was unsuccessful in what appeared to be an attempt to get the fish. After this the crab returned to its burrow and did not go back again.

Experiment J.—The conditions were the same as those of Experiment I, except that the stick was pushed down into the sand until the fish was 4 cm. from the surface of the ground. Flies were thickly clustered about the food when a crab approached. This individual did not reach up and take the fish, but made an attack by jumping quickly at the food, striking it with its claws and jumping away, after which it moved off quite a distance. Then the ocypoda repeated this same behavior several times, until the flies were scared away, when finally it reached up, standing on the last two pairs of walking appendages, and began to eat. The stick was then raised again until the fish was 50 cm. from the sand, after which the same crab returned, but did not reach up. The fish was soon abandoned. Several times during the afternoon a small crab attempted to climb up, *i. e.,* put its claws against the side of the stick and raised itself, but was never successful in reaching the food.

While it can hardly be claimed that any of the above experiments furnish conclusive proof that *Ocypoda* is stimulated by odor, experiments 5 and H point strongly in that direction. The behavior in most of the rest of the experiments may be explained by any one of the following hypotheses: (1) That *Ocypoda* reacts to odor. (2) That opaque objects are distinguished as a result of the difference between the intensity of light on the object and the region surrounding. (3) That *Ocypoda* actually has vision. (4) That any two or all of these factors determine the behavior.

As we shall see later, the author was unable to obtain any evidence that *Ocypoda* has vision. It might be held by those who do not admit that crustacea see with their eyes or react to odors, that *Ocypoda* approaches food and other objects merely by chance, but those who have observed this interesting crab can not for one moment believe this to be the case.

EYES.

Anyone who, for the first time, sees an ocypoda running over the white sand is forcibly impressed by the prominent and relatively large stalked eyes which, being almost black in color, form a striking contrast to the rest of

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the body. Who has not been tempted to say, when he walks along the beach and sees these crabs in the far distance scampering in haste toward their burrows, that they have a keen sense of vision? Thus far, however, we have no proof that crustacea have vision—that definite pictures, such as we know are formed in the eyes of the higher vertebrates, occur in the eyes of these invertebrates.

The stalked eyes of *Ocypoda* are capable of considerable movement. They may be dropped laterally into grooves under the anterior edge of the carapace, where they are quite well protected. Besides this lateral movement I have noticed individuals move the eye-stalks backwards and forwards while sitting perfectly still on a level surface. It is of interest to note that individuals when starting down their burrows (they always go down sideways) drop the foremost eye-stalk into the groove under the carapace, leaving the hindmost one erect. The advantage of this procedure can easily be seen. When the eyes are erect the angle of possible movement toward the sagittal plane of the body is very small, so that in going down the burrow, if the eye-stalk were kept erect there would be danger of its being forcibly bent or broken off by striking against the walls of the burrow. The hindmost eye-stalk, however, does not run this danger. Furthermore, it is not probable that the crab receives any very definite light stimuli through the eye on the side presented to the dark end of the burrow, while the other eye undoubtedly serves as a means of detecting any lessening of the intensity of light at the opening of the burrow which might be caused by the approach of an enemy.

In *Ocypoda* the part of the eye sensitive to light extends over quite a large surface and covers much of the distal end of the stalk. It is not evenly distributed; the largest surface exposed is on the anterior side; the next largest is on the outer sides; the next on the posterior side and the smallest is on the dorsal surface (fig. 7). This distribution of the sensitive surface corresponds with the attitudes commonly assumed when a crab is watching. In the majority of cases it presents either the entire surface or the side of the body toward the object in question; less frequently the posterior surface. The dorsal surface of the eye which has the smallest sensitive surface is no doubt used the least, since no enemies approach from above and since the food is on the ground. As we shall see below, this crab seldom reacts to the movements of objects directly above it.

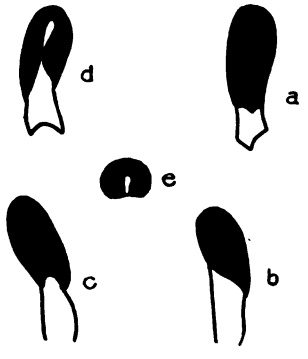

FIG. 7.—Surface of eye of *Ocypoda*. *a*, anterior view; *b*, posterior view; *c*, outer side; *d*, inner side; *e*, dorsal side.

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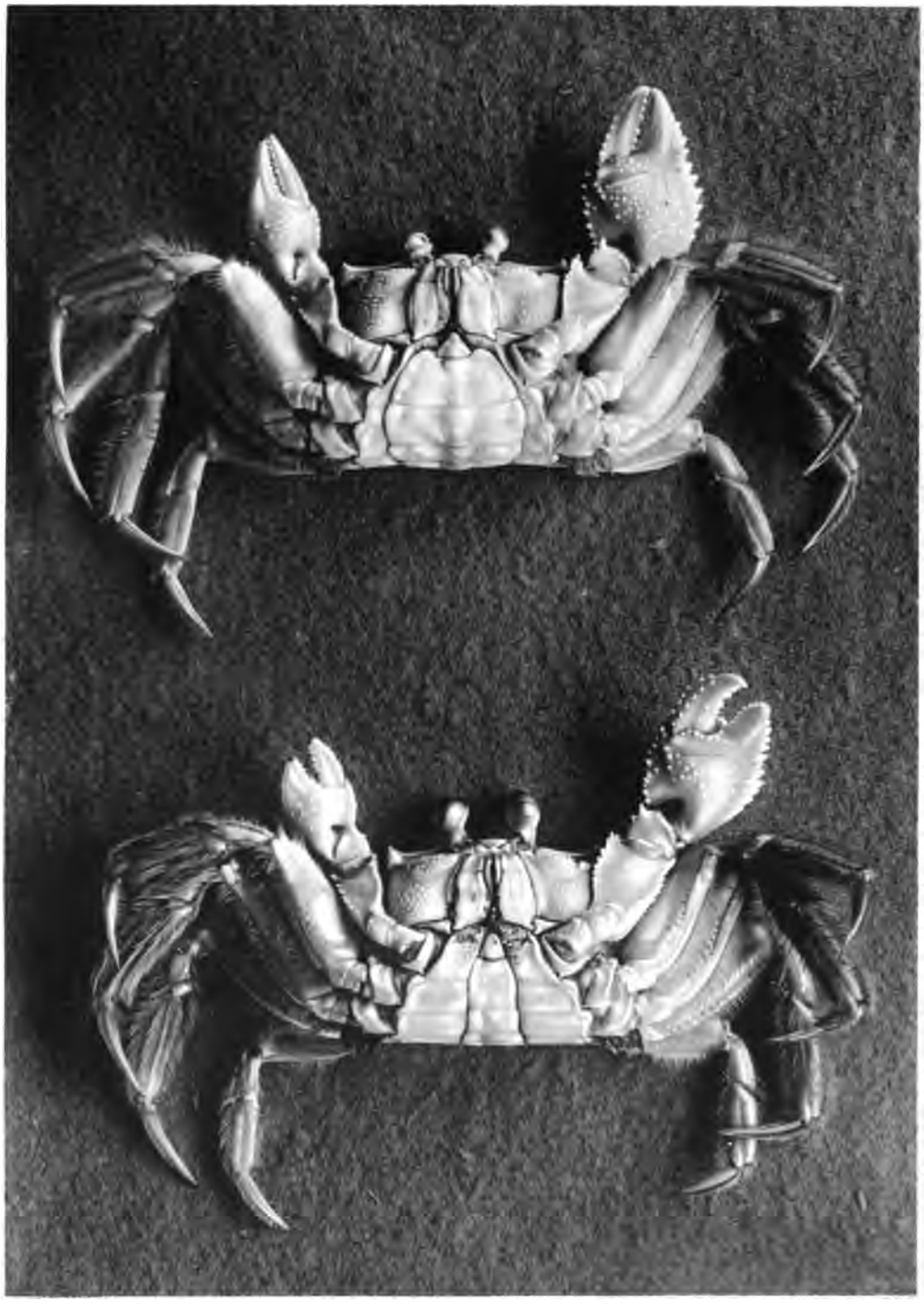

Ocypoda Arenaria. Female above. Male below. Ventral views.

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The so-called compensatory movements of the eye-stalks, such as have been described for other Crustacea, occur in *Ocypoda* when it is tilted either from right to left or anteriorly and posteriorly. The angle in the latter case, however, is quite small. It was noticed that when an individual was tilted forward or backward until the limit of movement was reached the eye-stalks were immediately lowered into their sockets. Another interesting observation was the following: When an ocypoda was picked up, the normal position with reference to the ground being maintained, it almost invariably dropped the eyes into the grooves, but when the crab was lowered again the eyes were raised as soon as the legs were allowed to touch the ground. In these experiments I kept hold of the crab even after it had been placed on the floor. Occasionally the eyes were raised in mid-air, not while moving up or down, however. The eyes are usually drawn down into the sockets when they are touched by the experimenter, and in the case of some individuals it was found that the same behavior was brought about when the crab was scratched with a pointed instrument along the middle of the carapace. There is considerable variation among different individuals with respect to the reaction from scratching, but in the same individual the result is quite constant.

Ocypoda lives along wind-swept shores and the wind seems to have no ill effect on the eyes. Even in a strong gale the eyes are seen standing erect, apparently unaffected. An attempt was made to cause individuals to lower the eye-stalks by blowing suddenly and sharply upon them, but it was not successful. In the case of the land-crab (*Gecarcinus*) the eyes were dropped immediately when the same experiment was tried upon them. It was found, however, that when an ocypoda was brought close up to the mouth of the experimenter and warm air was gently breathed on the eyes they were immediately drawn into the sockets. They remained erect when the crab was brought close up to the mouth without breathing on them.

There is no doubt that *Ocypoda* can distinguish a large object, such as a person, many yards off (at least 50 yards), as any one can testify who has seen these crabs run away on the approach of man. By this statement it is not meant that this crab has vision, that it sees things as human beings do, although I would not deny the possibility of imperfect pictures being formed on their eyes, but that its eyes are sensitive to changes in intensity of light and that it is able to see the outlines of objects where the contrast in the amount of light reflected by the object and that reflected by the surroundings is great enough.

While *Ocypoda* can see objects which are not moving, as the experiments D and E prove and as frequent observations of individuals approaching objects indicate, its behavior shows that the eyes are much more sensitive to objects in motion.

The following interesting performance, which was witnessed from the window of a laboratory built partly on the beach and partly out in the water, shows how well *Ocypoda* reacts to moving objects. One of the most

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common fish around the shores of Loggerhead Key is the gray snapper, *Lutianus griseus,* which patrols the waters close to the bank in search of food. Besides this rather large fish there are also schools of a very much smaller fish mentioned above, *Atherina laticeps.* These two species ordinarily occupy rather definite positions with reference to the shore line, the atherinas close in and the gray snapper farther out. The latter, however, prey upon the former and frequently make excursions shoreward, driving the atherinas into the surf and finally out of the water upon the beach, where they flop about helplessly. During the chase the gray snappers often flounder in the surf, making considerable noise. When this occurs, almost immediately ocypodas, if there are any out on the beach, run down and capture the little fish, returning with them to their burrows. They travel fast and in a straight line to their prey, leaving no doubt in the mind of the observer that the eyes are stimulated by the movements of the atherina.

I have frequently brought about this same reaction by throwing small fish from the window of the laboratory upon the sand below, in which case the behavior would be the same as above, showing that the noise produced by the gray snapper in the surf is not the only stimulus, if it is any at all, that attracts the crabs.

It might be claimed that the ocypodas reacted to the odor of the fish, but this is probably not the case, since the olfactory sense is not very well developed and since, when pieces of coral are substituted for fish, the behavior is the same up to a certain point. They will run directly to the coral, often pick it up, but seldom take it to the burrow.

In order to thoroughly test the influence of odor in the throwing experiments the hands were thoroughly washed and ten clean chips of wood were taken in the left hand and ten fish in the right hand. These were then thrown alternately to the crab, with the result that the chips were run after as if they were food. They were always examined, but not taken away.

To prove that the ocypodas did not react through the tactile sense as a result of the jarring of the sand when the objects were thrown upon it, another experiment was tried. An atherina was tied to a long thread and was thrown from the window in such a way that it would come within about 10 cm. of the sand, but would not touch it. Immediately an individual would run directly toward the fish, but finding nothing on the ground would attempt to capture the shadow cast by the fish. Failing in this the ocypoda would usually remain still for some little time, apparently watching, and would then make another jump at the shadow. After several trials, during which it would move away some distance and then return, the crab would go back to its burrow or begin feeding along the drift line. If then the bait was drawn up and after an interval of one or two minutes, was thrown again, the same behavior would be repeated by the original individual. Finally, if the experiment were repeated many times the crab would no longer react by running toward the shadow.

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The results of these experiments and observations leave little doubt that in Experiment F the movement of flies around the coral was a factor in determining the behavior of the crab.

The eyes of *Ocypoda* are stimulated much more strongly by moving objects and probably also by still objects on days when the sun is shining brightly than when it is cloudy; also much more during the middle of the day than early in the morning or late at night. It was found that the approach of man on cloudy days did not cause the crabs to retreat to their burrows as quickly as on days when the sun was shining brightly; also that they did not run as promptly after fish thrown to them early in the morning or late in the afternoon as they did after those thrown during the brighter part of the day.

During the night-time it was found that *Ocypoda* would easily approach a man lying on the sand and even crawl up upon him. The writer has had them enter his pockets and on several occasions has received their rather severe pinches. They show but little fear at night, when the contrast in intensity of light on objects is small, but in the day-time such behavior does not occur or at least very seldom.

Bethe (1895, 1897) has observed that when a light is directed against the eye of *Carcinus mænas,* or when a dark object is placed in front of the eye, the crab reacts by a movement of the first pair of antennæ. Such a movement does not take place in the case of *Ocypoda,* but it was found that when a dish containing several individuals was brought from the direct sunlight outside of the laboratory into the subdued light inside, they reacted by a sudden jump the moment the shadow of the door was reached and that when the dish was taken out they reacted again in the same manner as soon as the edge of the shadow was reached. After the change had been made rapidly and many times the crabs failed to react, but after allowing them to rest for a few minutes and then repeating the experiment the individuals began again to react.

While the anterior, posterior, outer lateral, and inner lateral surfaces are sensitive to the differences in intensity of light, the dorsal surface does not seem to be, or at least only slightly so (fig. 7). The writer was able to stand during the middle of the day at the open window of the laboratory mentioned in a previous section, without disturbing the crabs below in the least; not even the most exaggerated motions, such as the swinging of the arms or the waving of large objects, would cause them to run to their burrows or even move away. This was not a case of inhibition, for the same movements performed on the sand by the experimenter at the same distance, or a much greater distance, always caused a run for shelter.

Many attempts were made to study the behavior of *Ocypoda* after the eyes were cut off, but they would not live long enough after the operation to recover sufficiently from the shock. Much care was used in amputating the eyes, but in no case was it possible to keep the individuals alive for more

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than three days. The base of the eye-stalks is undoubtedly one of the most vital spots, and it is probably true that in nature the eyes are never pinched off without causing death.

I have seen many hundred ocypodas both at Loggerhead Key and Beaufort, North Carolina, and while I have often found specimens with one of the chelæ or one or two of the ambulatory appendages missing, I have never seen an individual with even one eye gone. Those ocypodas that had both eyes cut off did not react in any way to light or shadow cast upon them, and there is scarcely any doubt that the eyes are the only organs that are sensitive. Notwithstanding the severe shock resulting from the amputation of the eyes, individuals were often found that would be feeding at the end of 24 hours.

The effect of painting the eyes with a mixture of lampblack, shellac, and chloroform was also tried. When several coatings of this mixture were put on, these organs were not sensitive to light. It was found that immediately after the painting individuals were quiet, but that very soon they became more active and assumed the defensive attitude (plate 1, fig. c). As Bethe (1895, 1897) has observed in the case of *Carcinus*, they were well able to protect themselves from normal individuals. On land they were much more sensitive to tactile stimuli than ordinarily, and in the aquarium they were much more sensitive to the vibrations of the water produced by striking the glass than normal ocypodas.

The angle of compensation when a crab was tilted was somewhat less than the normal, confirming the observations of Clark (1896) and Prentiss (1901) for the fiddler-crab and those of Lyon (1899) for the crayfish. The blackening of the eyes seemed to have no effect on the maintenance of equilibrium and did not prevent the ocypodas from running about in a normal manner when stimulated.

The most evident change in the behavior under these abnormal conditions was the lack of reaction to a sudden increase or decrease in the intensity of light, the absence of any reaction to moving objects and the failure to approach objects as they ordinarily do when the eyes are not painted.

Several experiments were tried to determine if the eye of *Ocypoda* reacted to one color more than to another. For this 18 atherinas were used; 6 were stained red, 6 were stained blue, and the rest were left unstained. These were thrown alternately to an ocypoda, but there was no special difference in the behavior toward the different ones.

An attempt was made to see if they would form an association between colors and food made distasteful in some way. Many experiments using stained atherinas soaked in the acid juice of the lime were tried, but these did not give any results indicating an association of color with distasteful food.

Quite a number of experiments with red and violet color-filters made of celloidin were tried, but these yielded no definite results.

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In conclusion it may be said that the eyes of *Ocypoda* are the most highly developed of crustacean eyes; that they are stimulated by differences in the intensity of light when these are large enough; that they are quite sensitive in this respect; that they do not react to different colors; that they aid much in the search for food, in the detection of enemies, and in the accuracy of locomotion. My observations and experiments afford no proof that *Ocypoda* has vision, such as exists in the human eye, but its behavior leads me to believe the eyes are so well developed that it almost amounts to the same thing. While they probably do not see the color of an object or the finer characters of its surface, they undoubtedly see its outlines and possibly some of the more evident irregularities of the surface, made evident by the differences in lighting.

COLOR-CHANGES.

It has long been well-known that some species of Crustacea change in color when placed under different conditions, but these observations seem to be almost entirely confined to those forms that live in the water. Certain species of *Hippolyte, Palæmon, Crangon, Idothea, Nika, Gammarus,* and others have been studied, but as far as I know observations on the color changes of only one of the Brachyura have been made.

Color changes or pigment migrations have been investigated in the vertebrate skin, especially that of lizards and frogs, in the hypodermis of crustaceans, in the retina of vertebrates, crustaceans, insects, and cephalopods. Various causes have been suggested which might produce these changes, such as light, heat, color environment, emotional states, and other nervous conditions.

The carapace of *Ocypoda* is very lightly colored and shows practically no color-pattern. Any pigment which it does contain apparently undergoes no change when exposed to different intensities of light and heat, but the hypodermis underneath is rich in dark pigment-cells. As the carapace is almost colorless, and is translucent, the pigment-cells of the hypodermis, arranged in the form of a pattern, show through very plainly under certain conditions.

The writer had been observing ocypodas and experimenting with them for a considerable period before it was seen that the color-pattern under the carapace changed from time to time, although it was often noticed that some individuals had a definite pattern, while others were almost free from it. This lack of color in some specimens was supposed to be due to the fact that they had recently molted, until finally, while testing the effect of different color-screens on the behavior of *Ocypoda,* new light was thrown on the subject. In this experiment 4 ocypodas were placed in a box which had colored windows made of gelatin. After being confined for about an hour they were taken out and by chance placed in a dish of cool sea-water where, much to my surprise, they began to turn dark, showing a very distinct color-

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pattern. Three of these were then put in a glass dish and placed in the direct sunlight on the white sand. Ten minutes later these had lost nearly all their color, showing almost no markings. The other one was kept in the diffuse light of the laboratory and did not change in color. It had the same dark pattern the next day. These observations left no doubt that the color-pattern under the carapace was subject to considerable change when placed under different conditions of light, heat, or moisture, and experiments were then undertaken to determine what factors brought this change about.

Experiment I.—Three small ocypodas, quite light in color, were taken from the trap and placed in the box with colored windows at 3^h 15^m p. m. The box was kept in the bright light near a window until 4^h 50^m p. m., when it was found that the crabs had not changed in color. So far as these experiments were concerned there was no indication that the colored windows had anything to do with the formation of a color-pattern. However, it is not claimed that careful experiments with color-screens might not show that certain parts of the spectrum may be more effective in bringing about color changes than others. After the specimens were removed from the box they were put into sea-water and kept in the laboratory, where they began to turn dark at once. They were then removed to a dry dish, where they continued to grow darker.

Experiment II.—Two rather dark ocypodas were exposed to the direct sunlight for 15 minutes and became very light in color. They were then put into a dish of sea-water and placed in a rather shaded part of the laboratory (8^h 12^m a. m.). A dark plaid pattern soon made its appearance, after which the crabs were put in the direct sunlight on the white sand still immersed in sea-water (8^h 22^m a. m.). At 8^h 30^m a. m. they were much lighter in color and at 8^h 49^m a. m. they were almost colorless. The specimens were then put in a photographic dark-room (8^h 50^m a. m.), still immersed in sea-water. To my surprise (believing at the time that bright light was the cause of blanching) at 10^h 45^m a. m. they were still almost colorless. However, upon being put in a dry dish and placed in a shaded part of the laboratory, they became dark after a few minutes.

These experiments show that the appearance and disappearance of the color-pattern is not a simple process, but that it may be brought about by one or several factors.

Experiment III.—In this experiment the same individual was used that was kept in the laboratory in Experiment I. It was dark in color. It was immersed in sea-water and exposed to the direct sunlight (8 a. m.). At 8^h 23^m a. m. the specimen had not changed in color to any appreciable degree and at 8^h 30^m a. m. it was possibly a little lighter. The crab was then placed in a dry dish (8^h 31^m a. m.) and left in the sunlight. As would be expected, at 8^h 35^m a. m. the specimen was still light. At 8^h 40^m a. m. it was put in a dish covered with a black tray and placed in the photographic dark-room. When examined at 10^h 45^m a. m. it was found to be still devoid of a color-pattern, as in the case of Experiment II. When the individual was put in sea-water and placed in a shaded part of the laboratory it became quite dark after a few minutes.

Experiment IV.—A rectangular glass dish, 35 cm. in length, 25 cm. in

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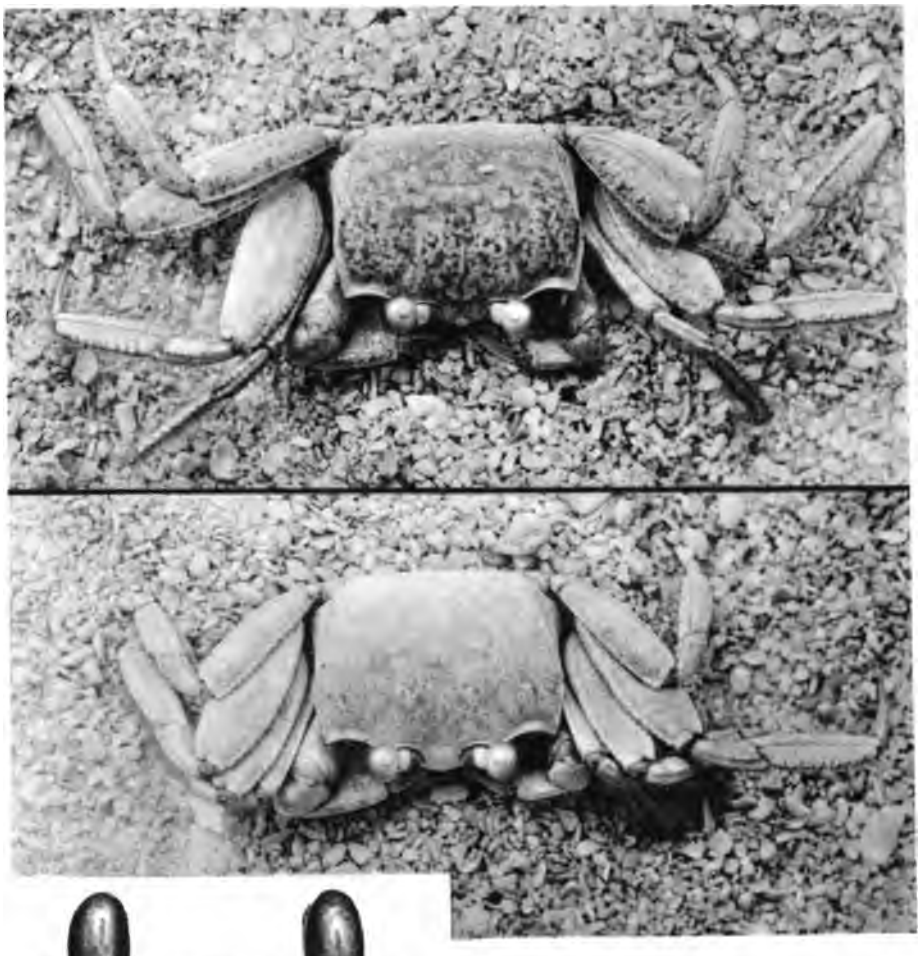

Upper figure. Ocypoda kept in diffuse light of the laboratory.

Central figure. Same individual exposed to direct sunlight for 10 minutes.

Lower figure. Otocysts of Ocypoda.

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width and 7 cm. in depth, was divided into two equal parts by a partition in the middle. One of these parts was lined and also covered with black glass. The other part was left without lining except that the side of the partition was covered with white bristol-board. The cover was made of ordinary clear white glass. Sea-water was poured into the dish until it was 2.5 cm. deep and then two crabs with dark plaid patterns were put in—the darker of the two in the light side, the other in the dark side (8^h 35^m a. m.). The dish was then placed in the direct sunlight until 9^h 47^m a. m. Both were equally light in color. (Temperature of water 45° C. at end of experiment.) The results indicated that heat was the factor which brought about the loss of color, so the following experiment was tried:

Experiment V.—Two dark specimens of practically the same shade were used. One was placed in a dish of water kept at a temperature of 45° C. (temperature of the water in Experiment IV after exposure to the sun), the other in water whose temperature was 23° C., and both were put in a shaded part of the laboratory; they were left for 15 minutes, after which the former became decidedly lighter, while the latter did not change.

Experiment VI.—The same experiment was repeated, except that the temperature of one was kept at 44° C. and the other at 23° C. The result was the same.

The last three experiments undoubtedly show that a temperature as high as that on the sands of Loggerhead Key will cause a loss of color when the specimen is not exposed to bright sunlight. These results received further confirmation in the following experiment:

Experiment VII.—Two dark-colored ocypodas were used. At 2^h 35^m p. m. one was put in a dry dish over a sand-bath, kept at 36° C., in a shaded part of the laboratory, and the other was placed under the same conditions, except that it was not heated. (Temperature of air 24° C.) At 3 p. m. the former had almost lost its color-pattern, while the latter had not changed.

Experiment VIII.—A light-colored ocypoda (1) which had its eyes painted with shellac and lampblack (it did not react to shadows) was put in a dish of sea-water and placed in a shaded part of the laboratory at 7^h 40^m a. m. Another light-colored one (2), whose eyes were painted (it was not quite as light as the other), was put in the direct sunlight without water (7^h 30^m a. m.). At 7^h 50^m a. m. (2) was brought into the laboratory, put in a dish of sea-water, and placed in the shaded part of the laboratory. Crab (1) was taken out of the sea-water, put in a dry dish, and then in the shaded part of the laboratory (7^h 56^m a. m.). Finally (2) was taken out of the water and left in the shaded part of the laboratory (8^h 06^m a. m.). Throughout these changes neither (1) nor (2) changed in color, and at 8^h 21^m a. m. they were in the same condition. This experiment affords quite conclusive proof that the eye of *Ocypoda* must receive light stimuli in order to bring about a distal migration of pigment under the carapace, *i. e.*, in order for the color-pattern to appear.

Experiment IX.—In this experiment two ocypodas whose eyes had been painted 24 hours before were used. (They did not react to light.) Both of the specimens were light in color, although kept in the shaded part of the laboratory (6 a. m. Temperature 23° C.). The paint was removed from the eyes of one of the individuals and in less than half an hour it became

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darker. At 7^h 45^m a. m. it was much darker, showing a distinct plaid pattern, while the other ocypoda was still as light in color as at the beginning of the experiment. These results I consider as evidence that the stimulus given to the eye by light is an important factor in bringing out the color-pattern, since the temperature was practically constant throughout the experiment. It might be claimed that disturbances in the nervous condition of the specimen affected the results, but in the light of other observations this does not seem probable.

Experiment X.—A specimen with a very dark color-pattern was used and an attempt was made to bring about a color change by frightening it. The crab was stimulated several minutes by moving the hand in front of it. This caused the specimen to run about very vigorously, but there was no change in color. This method of stimulating the crab was continued until it showed signs of exhaustion, but still there was no change in color. When it was subjected to a strong electric shock two of the ambulatory appendages were broken off, but even this had no effect on the color-pattern. Finally the ocypoda was etherized for 2 minutes until it was perfectly quiet, and then allowed to revive, but this brought about no change in color pattern.

The results obtained in Experiments IV, V, VI, VII show conclusively that the high temperature on the surface of the sand, which is a result of the exposure to the direct sunlight, brings about a proximal migration of the dark pigment under the carapace of *Ocypoda* (plate 4). Accordingly the following two experiments were tried, in order to determine if the direct sunlight would cause a blanching of the carapace when the temperature was kept comparatively low.

Experiment XI.—An ocypoda which showed a dark color-pattern and which had been kept in the diffuse light of the laboratory (temperature of air 33° C.) was used. It was placed in a dish filled with sea-water and covered with a glass plate. The outside of the dish was then covered with a piece of heavy cloth saturated with alcohol (unfortunately no ice was at hand) and the whole thing was put in the direct sunlight on the sand at 2^h 04^m p. m. The evaporation of the alcohol kept the temperature of the water at 35° C. At 2^h 35^m p. m. the specimen was still almost as dark as at first. The slight loss of color was probably due to the 2° increase in temperature.

Experiment XII.—Using the same individual, the above experiment was repeated after removing the cooling cloth (2^h 40^m p. m.). At 2^h 56^m p. m. the temperature of the water was 45° C. and the specimen had become very light.

Experiment XIII.—The ocypoda used in Experiments XI and XII was brought into the laboratory and placed in a shaded place (2^h 56^m p. m.; temperature of air at 33° C.). At 3^h 11^m p. m. it had regained its original dark color.

Experiment XIV.—Experiment XI was repeated under the same conditions, except that the specimen was put in the darkness of the photographic dark-room. Although the temperature was kept at 35° C. by the above cooling device, the crab soon lost its color-pattern and dark color, a change undoubtedly due to the absence of a light stimulus on the eyes.

Often during the above experiments individuals were observed to grow

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perceptibly darker after removal from water into a dry dish. This color change was undoubtedly due to a decrease in temperature resulting from the evaporation of water from the surface of the specimen.

Many observations were made on ocypodas living under natural conditions. During the middle of the day, when the sun was shining brightly, specimens seen feeding on the sand were usually light in color, but occasionally dark individuals were found. These latter had probably just emerged from their cool, shady burrows (the entrance not closed). During the late hours of the afternoon and on cloudy days, however, most of the ocypodas feeding along the beach were dark in color, although occasionally a very light one would be seen. Probably the latter had been buried in a closed burrow which was dark.

The following interesting observation of the effect of light on the pigment-cells of the eye was made: A small ocypoda was kept in a box, the bottom of which was filled with sand to a depth of 10 cm. There was a crack left between the bottom of the box and one of its sides, into which the direct sunlight shone. The specimen had burrowed to the bottom of the box in such a way as to have one eye exposed to the direct sunlight while the rest of the body, including the other eye, was in comparative darkness. When this individual was taken out the eye which had been exposed was almost devoid of black pigment, while the other one was black as usual. The color-pattern under the carapace, however, was neither very dark nor very light. After 15 minutes in the diffuse light of the laboratory both eyes were as black as usual.

While no experiments were tried to determine the effects of light and heat on the pigment migration in the retina of the eye, it is probably true that the blanching in this case was due to the heat of the direct sunlight and not to the light itself. The medium dark coloration of the hypodermis under the carapace may be explained by the facts that the eye was stimulated by light and that the rest of the body was exposed to a medium temperature, two conditions which, according to my experiments, would result in a medium dark coloration.

DISCUSSION OF RESULTS.

Brooks and Herrick (1889) working on *Alpheus* and *Palæmonetes,* P. Mayer (1879) on *Idothea,* and Herdman (1894) on *Virbius varians* find that the stimulation of the eyes by light is an important factor in color change. Malard (1892) tells us that in the case of *Hippolyte varians* the intensity of the light has an effect on the color, and that in many crustacea the stimulation of the eye by light and the color environment are factors. In *Idotea tricuspidata* Matzdorff (1882) finds that variations in temperature, light, and density of water do not cause color change, but claims that the latter is a "sympatische Wechselfärbung" which varies with the surroundings. Pouchet (1872), in his work on *Palæmon* and *Leander serrator,* lays special

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stress on the stimulation of the eye by light, but also finds that toxic substances and to some extent electric shocks may bring about color change. In a later paper (1876) he discusses in particular the influence of the background on color change. According to Fritz Müller (1883) alarm causes the color of the male of a Brazilian species of *Gelasimus* to change, and this is the only observation I know of on any brachyuran. Temperature does not seem to be a factor in color change according to the above investigators, but Jourdain (1878) working on *Nika edulis* finds that heat affects the color. Not only has he observed that low temperature causes a blanching, but he also tells us that stimulation of the eye by light and internal stimuli are factors in color change. The only other observations on crustacea in which temperature is said to play a part in the color changes are those of Gamble and Keeble (1900). These investigators find that the color of *Hippolyte varians* is affected by ether or the recovery from its effect, by electrical shocks, by cold, and by light stimuli through the eyes. In *Anolis,* according to Carlton (1903), the green state is brought about by darkness, withdrawal of circulation, and possibly the cutting of nerves. Specimens in narcosis from ether, those treated with nicotine, and those which are dead, are green in color. Carlton believes that the green state represents the resting condition of the melanophores and the state to which they return when they no longer receive stimuli. This green state seems to correspond to the blanched condition of *Ocypoda,* being brought about by some of the same factors.

The crustacean literature does not seem to afford any extensive investigations of color changes in land-crabs such as have been made in the case of the lizard, although Gamble and Keeble (1900, 1904) have published two papers which promise to be the beginning of a very thorough study. It is of considerable interest, I think, to find that the results of my work on *Ocypoda*—which lives under much the same conditions as *Anolis carolinensis,* worked on by Parker and Starratt (1904), and especially *Phrynosoma blainvillei,* studied by Parker (1906)—agree in many respects with the results obtained by these two investigators.

The experiments so far performed yield no results which would indicate that color environment or nervous condition are responsible for changes in color observed through the carapace of *Ocypoda*; nor does the immersion in water seem to be a factor, except in so far as the temperature of the water is concerned. Changes in the intensity of light and variations in temperature are undoubtedly the main stimuli, if not the only ones, which bring about the proximal migration of pigment resulting in a dark color-pattern or the distal migration resulting in a disappearance of the color-pattern.

In the absence of light when the temperature is anywhere between 22° C. and 45° C., and undoubtedly when it is lower or even higher, a light coloration occurs.

Generally in diffuse light, and even direct sunlight, a dark coloration appears, provided the temperature is not too high.

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Usually at low temperatures, not above 35° C., a dark coloration occurs, provided the eye is stimulated by light.

At high temperatures, above 35° C., a light coloration is the rule, and it occurs independently of the intensity of light.

The temperature limits given above are those obtained from a study during the hot summer months, but it may be that in winter, when the average temperature is much lower, the limits would be different.

These results may be stated in another way. Dark coloration occurs at comparatively low temperature in diffuse or direct sunlight.

Light coloration occurs at comparatively high temperatures when light is absent.

Light coloration occurs at comparatively low temperatures and at medium temperatures when light is absent.

Light coloration occurs at comparatively high temperatures in diffuse or direct sunlight.

The blanching of individuals on the sands of Loggerhead Key is probably due to the high temperature alone. (See plate 1.) The results of Experiment XI indicate that it is not a reversed light reaction. On the other hand, the blanching in the photographic dark-room may be due to the absence of light alone.

The dark coloration of individuals occurs only when the eye is stimulated by light, and then only when the temperature is comparatively low. The indications are that it is not the result of the direct action of light on the pigment-cells or on the nervous system.

EQUILIBRATING ORGANS—"AUDITORY ORGANS."

For many years an auditory function was ascribed to certain organs found in the basal joint of the antennules in decapods, but since the work of Bethe (1895, 1897), Beer (1898, 1899) and Prentiss (1901) we have strong evidence for the assumption that the so-called "auditory organs" do not have the auditory function, but that they are organs which are important in the maintenance of equilibrium. So far as I know we have not as yet any good evidence that the Crustacea hear, and in those cases which have been recorded the supposed reaction to sound was probably due to tactile stimuli.

Although Prentiss (1901) stated in his paper on "The Otocyst of Decapod Crustacea" that *Gelasimus pugilator,* a brachyuran decapod, living much of the time on land, did not react to sound-waves, I was much interested to see if such an active and highly developed land-crab as *Ocypoda* was able to hear.

The "auditory organs," or otocysts, as I shall call them, are situated in the basal joint of the antennules, as in nearly all the decapods (plate 4), and they are partly protected by the rather broad but short rostrum.

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In order to determine if *Ocypoda* would react to sound-waves the following experiments were tried: A flute was played upon and large stones were hit together while the observer was hidden 12 feet away, but no movement could be seen that would indicate that the ocypodas were stimulated. The report of a pistol produced no apparent effect. During a heavy storm the peals of thunder were deafening, but several ocypodas which were along the beach did not return to their burrows nor cease their feeding. These experiments and observations indicate that *Ocypoda* does not hear, but they are by no means conclusive, and a series of such careful experiments as those performed by Fielde and Parker (1904) on ants and Yerkes (1905) on the green frog (*Rana clamitans*) would well bear repeating before it should be said that *Ocypoda* does not react to atmospheric sounds. Although it does not seem probable, it might then be found that notes causing a very small number or a very large number of vibrations of the air per second had an effect.

Ocypoda while eating produces a grinding sound by the movements of its mouth-parts, and at times it also makes a noise resembling the "peep" of young birds, but I have no proof that these sounds stimulate the otocysts of other crabs.

Prentiss (1901), in his review of the crustacean literature (p. 228), has cited two well-known examples of noises, the one a case of stridulation in *Palinurus vulgaris*,[1] described first by Möbius (1867) and later (more correctly probably) by T. J. Parker (1878), and the other the pistol-like report of *Alpheus* described by Goode (1878). To these may be added the stridulation of *Ocypoda*, although I have never been fortunate enough to hear it. Often at night I have stayed on the beach among the feeding ocypodas in the hope of hearing the stridulation, and I have listened at the entrance of the burrows which were occupied by individuals. I have good reason, however, to believe that the stridulating noise is made, since I have often seen ocypodas go through the motions that would produce it when they were attempting to gain possession of a burrow occupied by another specimen.

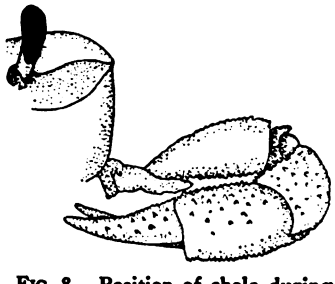

FIG. 8.—Position of chela during stridulation.

Along the inner surface of the palm of the cheliped in the individuals there is a row of fine tubercles (stridulating ridge, plate 3), which when the cheliped is bent, as shown in text-fig. 8, comes in contact with a process on the basal joint. By moving the distal part of the appendage from side to side the row of tubercles is rubbed against the process and a sound is produced. I have seen this movement frequently in the case of individuals

[1] Mentioned first by Leach in Malacostraca Podophthalmata Britanniæ, 1815.

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that seemed to be excited, and it was performed with great rapidity. There is scarcely any doubt that the sound is produced, but I have no reason to believe that other ocypodas hear it. However, the vibrations produced by the rubbing might easily be transmitted to the sand and thence to the sensitive tactile hairs on the ambulatory appendages of another individual, thus producing a tactile stimulus.

In Mier's (1876) paper it is stated that in one species of *Ocypoda* the stridulating ridge is absent in the very young individuals. I have examined many specimens of *O. arenaria,* the smallest 1 cm. across the carapace, but have always found the ridge present. It is of interest to note that the land-crab, *Gecarcinus,* which is found in abundance on Loggerhead Key and which lives under very similar conditions, has no stridulating ridge.

As has been pointed out by Prentiss (1901), it does not follow that an animal is able to hear because it makes a noise, and as yet we have no observation or experiments proving that *Ocypoda* or any other crustacean has audition.

Many attempts were made to repeat the experiments performed by Beer (1898) and Prentiss (1901), in which the behavior was observed after the removal of one or both of the otocysts. In every case in which both of these organs were removed the individuals did not live long enough to recover from the shock. As a general rule, even the removal of one otocyst caused such profuse bleeding that the specimen soon died. The behavior of operated individuals, however, was very similar to that observed by Prentiss (1901). Those ocypodas which had their eyes painted, so that there was no reaction to sudden changes in the intensity of light, retained their equilibrium as well as normal individuals. The only difference in behavior was their tendency to remain quiet. While the eyes undoubtedly assist in maintaining the equilibrium, they are not the most important organs in this respect.

The removal of one otocyst brought about some disturbance in equilibrium, part of which may have been due to the shock, but the removal of both otocysts caused very marked effects; individuals when placed on the sand usually turned one or more somersaults. While these disturbances may have been partly due to the operation, they were undoubtedly largely the effect of the loss of organs that regulate the equilibrium.

TACTILE SENSE.

While *Ocypoda* probably does not hear, the tactile sense is well developed and is a very important factor in regulating this animal's activities.

As would be expected, *Ocypoda* is quite sensitive to jars transmitted to the sand. I have often watched individuals which were part way down in their burrows, but not so far that the legs of one side might not be seen. Under these conditions, a movement of my foot in the sand or a step within 3 or 4 feet caused the specimen to react by a sudden movement, even when

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I was hidden from view. Often while observing ocypodas in the trap I have found that they did not move when a stick was waved in front of them, but as soon as it hit the side of the trap they would react either by a quick jump or a movement of the eye-stalks. However, there was considerable difference in the behavior of individuals, some being quite sensitive and others not so much so.

Ocypoda also reacts to vibrations of the water in aquaria, but it is not nearly so sensitive to these stimuli as to those caused by jarring the sand.

LOCOMOTION.

The locomotion of the Decapoda has been investigated by List (1897) and Bethe (1897), but both of these workers have confined their studies to those forms which live most of the time in water and which are not adapted to very active locomotion on land. The Ocypodæ, however, spend a large part of their lives on the beach sands and can travel for long distances at a considerable rate of speed. In fact, their movements are so rapid that it is often impossible to determine the order in which the various ambulatory appendages are used.

Bethe (1897) has observed that *Carcinus mœnas* ordinarily travels sideways, but that to a very limited extent it can move forward and backward. According to this investigator the locomotion sideways is directly sideways, and not oblique as List (1897) has described for decapods in general.

As in the case of *Carcinus,* ordinarily *Ocypoda* runs sideways and in a direction at right angles to the sagittal plane of the body. It seems to be much better adapted to locomotion in other directions, however, than any of the Brachyura. Unlike *Carcinus,* it will move obliquely sideways with considerable speed and will travel forward for long distances at a good rate. As mentioned in Experiment D, *Ocypoda* can move backward for quite a distance, but it does so slowly, and when a quick movement is required in that direction it usually jumps. On the whole it seems to be better adapted to life on land, so far as locomotion is concerned, than any other decapod.

Ocypoda usually runs toward an object with a considerable degree of accuracy. It often returns to its burrow almost directly in a straight line when disturbed by the approach of man, and I have often seen them accomplish this from a distance of 15 or 20 feet. This same accuracy is shown when they approach objects which have been thrown on the sand, although it is true that sometimes they fail to go more than two-thirds of the distance. So far as I have observed, individuals very seldom run beyond the mark.

Bethe (1897) on page 510 says: "Mann sicht daraus klar dass von einem 'Sehen' in unserem Sinne, von einer Perception der Lage und Entfernung des Gegenstandes, nicht die Rede sein kann." Bethe's statement

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that *Carcinus* does not see in the way we do is undoubtedly true also of *Ocypoda,* but I believe that the latter has, through the use of the eyes, a sense of position and distance; else how could it run so quickly and often so accurately after objects thrown on the sand several feet away?

Not only is *Ocypoda* quite accurate in returning to its burrow after moving away from it in a straight line, but it also returns accurately after running around in different directions on the beach. However, individuals differ much in this respect. The following observation showed very nicely how an ocypoda could return directly to its burrow even after feeding along the beach and showed also that it could return when the dark opening of the burrow was hidden. This crab had made its home so that the opening was in a hollow formed by the heel of a shoe and on this account the entrance was concealed (fig. 9). Starting from *A,* the specimen made its way leisurely to *B* (12 feet), feeding on the way; from *B,* it slowly went to *C* (10 feet) continuing its feeding; then the approach of a man caused the crab to run for its burrow (about 13 feet away), and it did so directly and accurately even though, as stated above, the entrance was hidden. Similar exhibitions of accuracy, when, however, the opening of the burrow was not hidden from view, were frequently observed. The young individuals are much less accurate in this respect, and while an observer is walking along the beach many of the small ones will be seen running about aimlessly as though lost, while the adults nearly always reach their burrows easily.

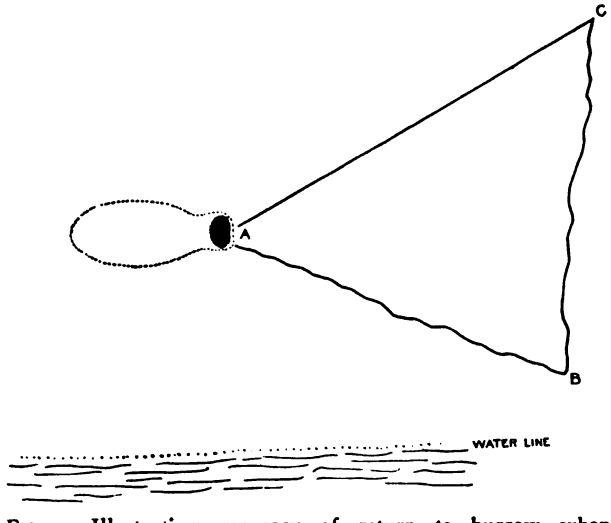

FIG. 9.—Illustrating accuracy of return to burrow when entrance was hidden from view.

While *Ocypoda* undoubtedly depends to a considerable extent on its eyes during movement toward a definite object or place, as is indicated by the inactivity of individuals with painted eyes, there are other factors which are almost equally important. The care which many of the older individuals take in preparing the surface of the sand immediately in front of the entrance to their burrows leads one to believe that they are sensitive to the contour of surfaces. Such a sense of the contour of surfaces has already

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been ascribed to *Pagurus* by Bohn (1903). Ocypodas are often seen carefully tamping down the mound in front of their burrows by means of the flat outer side of the large chela, making it round and smooth. Occasionally when there is a small hollow in the surface they will bring sand and fill it up. Sometimes I have seen individuals, which had apparently lost their bearings in the hasty return to their burrows, behave as though they were testing the surface of little mounds which were not situated in front of burrows.

Several factors contribute in bringing about the accurate return of these crabs to their homes. They are undoubtedly guided by differences in the lighting of surfaces, by tactile stimuli, by differences in muscular effort, and by stimulation of the equilibrating organs resulting from a tilting of the body.

BEHAVIOR TOWARD WATER.

While *Ocypoda* lives most of the time on land, it is absolutely necessary for it to go into the water occasionally. I am unable to say how long it stays in the ocean during the breeding season, but at other times, so far as my observations go, it remains there only a short time unless forced to do so by some enemy that prevents its return.

Adult individuals may spend hours in their burrows without going near the sea, but the young ones seem to be much more dependent on a fresh supply of water. This may account for the fact that their burrows are built closer to the water-line than those of the adults.

When an ocypoda is startled or disturbed while far away from its burrow it is very apt to run into the water, but even then it probably never goes out more than 4 or 5 feet from the shore. *Ocypoda* does not swim, but crawls along the bottom and is washed back and forth by the surf.

When undisturbed, *Ocypoda* goes down to the ocean now and then in order to moisten its gills with fresh sea-water; but at these times the individuals do not enter the water; they settle down about 6 or 8 inches from the water-line formed by medium-sized waves, with the ambulatory appendages of one side presented to the ocean and those of the other side firmly embedded in the sand. In this position they wait until an extra high wave washes over them and then return to the higher parts of the beach. Sometimes, after remaining in a place for a considerable period without being wetted by a wave, the crab will change its position to one closer to the water.

While *Ocypoda* does not live in the ocean much of the time, it is able to do so, as is shown by the following experiments: A large adult male was put in an aquarium filled with sea-water and left there for 6 hours. It was apparently in good condition when liberated at the end of this time. Another specimen left in the aquarium for 24 hours was also active when released. Other specimens placed in fresh water lived only for 5 hours and made frantic attempts to escape.

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Ocypoda is not able to live very long without water, although it may stay down in its damp, cool burrow for several hours. When in the direct sunlight without water it lives but a short time. Of 10 specimens placed in the sun in a wooden tub all but 3 had died after 4 hours' exposure. Other specimens kept in a dry aquarium in the laboratory and not exposed to the direct sunlight lived almost 24 hours. Although *Ocypoda* can live probably not over 24 hours in a dry place, it remains alive much longer in damp sand. Several specimens placed in an aquarium and buried to a depth of 15 inches in damp sand were alive and active at the end of 48 hours.

ENEMIES, DEFENSE, HIDING, SLEEPING, ETC.

On Loggerhead Key, *Ocypoda* does not have many enemies. The gray snapper and man seem to be the only large animals that molest them, but they are undoubtedly troubled by parasites and sometimes they are killed by their own kind. The writer has often seen gray snappers darting about close to the beach when an ocypoda has been driven into the water. As a rule the latter keeps just out of reach, but occasionally a young one will be snapped up by the fish. The large adults defend themselves fairly well when dropped into deep water among a number of snappers. Upon the approach of the fish the crab strikes out with its large chela in the same way that it does on land and this usually drives the gray snapper away. Eventually, however, if it does not crawl into shallow water its ambulatory appendages are bitten off one by one and the body is torn to pieces. Such observations can be easily made at Loggerhead Key, because the water is very clear.

Bethe (1897) has described what he calls the "Aufbäum Reflex" of *Carcinus mænas*. This attitude, he tells us, is brought about by stroking along the back or head and also by moving an object in front of the crab. In the case of *Ocypoda* a similar attitude is assumed and it is undoubtedly one of defense. The crab rises up on the distal segments of its walking legs, the chelæ are raised and spread for apart and the body proper is held well up above the surface of the sand. This defensive attitude is shown in plate 1, fig. c.

As a rule, when *Ocypoda* is disturbed by man it either runs into its burrow or, when hard-pressed, goes into the water; but this interesting crab has another way of concealing itself from man. Occasionally an individual is seen which, instead of trying to find a burrow or attempting to run into the water, will settle down in some little hollow, push its body backward into the sand, and then with its posterior ambulatory appendages throw sand over itself until most of the body is covered. Usually the eyes remain perpendicular, but sometimes they are dropped into their sockets.

Another condition in which *Ocypoda* is occasionally found is the resting or "sleeping" condition. I have seen a few individuals in this state during

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my walks along the beach. The body always rests on the sand, the legs are relaxed and stretched out, and the eyes are down in their sockets. Unless the sand is jarred too much by the approach of the observer, they lie perfectly still and do not react to changes in light intensity caused by the movement of an object in front of them. They may be even picked up before they show signs of activity. Upon one occasion a piece of meat on the end of a reed was moved within about 5 cm. of the mouth-parts, but this brought forth no reaction nor did the crab react when the meat was held as close to the mouth-parts as possible without touching them. When, however, the appendages of the mouth were touched by the food, they began to move slowly and then faster; after this the eyes came up, the ambulatory appendages assumed the position necessary for locomotion, and finally the chelæ seized the meat.

While *Ocypoda* does not normally exhibit what has been called the death-feigning reaction, or, as Bethe (1897) has called it, in the case of *Carcinus,* the "Starrkrampf reflex," it does so sometimes when placed upon its back and held in that position for a minute or so.

MEMORY.

Since the appearance of Bethe's (1898) classical paper on the nervous system of *Carcinus mœnas,* in which he compares this crustacean to a reflex machine and denies it the ability to learn, several papers have appeared which furnish abundant proof that some crabs are able to profit by experience and are even capable of forming habits. Yerkes (1902) investigating *Carcinus granulatus,* Yerkes and Huggins (1903) studying the crayfish *Cambarus affinis,* and Spaulding (1904) working on the hermit-crab *Eupagurus longicarpus,* have found that these crustacea form associations.

I hoped that *Ocypoda* would be a favorable subject for a quantitative study of habit formation, but as far as my experiments have been carried this does not seem to be the case. *Ocypoda,* we have seen, is a very active crustacean; its eyes are very sensitive when compared to those of other crabs; it is easily frightened, and when in this condition either runs away rapidly or remains perfectly still, failing to behave normally; when placed in a labyrinth with a solid bottom it usually scampers away from the hand that has released it and then often settles down in a corner without attempting to escape, or tries in vain to dig a burrow; failing in this it tries to climb; when the bottom of the labyrinth is made of sand it usually digs a burrow, goes down in it, plugs up the entrance, and stays there for a considerable time.

For the reason just mentioned it has been found very difficult to devise labyrinths which would be satisfactory, and the data accumulated on the length of time required for individuals to escape are probably not very trustworthy information concerning the rapidity with which *Ocypoda* forms a habit.

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Several different kinds of labyrinths were used, some of them similar to those employed by Yerkes (1902) and Yerkes and Huggins (1903), but these had to be reversed in the case of *Ocypoda,* because when the latter is disturbed it always runs away from the water. All the observations were made while the observer was practically hidden, and healthy active individuals were chosen.

It was found that labyrinths built of wood and closed up except at the exit were so dark that individuals would hide in them for hours at a time without attempting to escape, and that also labyrinths much more complex than those used by Yerkes and Huggins were of no use, on account of the length of time required for the crabs to find the exit.

A labyrinth like that used by Yerkes (1902) in his experiments with *Carcinus granulatus* was made, but glass plates were substituted throughout for the wood, so as to allow plenty of light to enter. It also had a glass bottom and top and was placed on the beach near the water, properly protected from any disturbance by the movements of people. The glass bottom was covered with a layer of sand about 1.5 cm. thick, and a screened pen was built around the exit so that the specimens could not escape entirely. It was found that individuals placed in this labyrinth usually only spent a short time in hunting for the exit; then they tried to dig a burrow, and failing in this they attempted to escape by climbing. Finally they usually settled down and remained quiet, so that they furnished no data bearing on the object of the experiment.

Finding that individuals nearly always made some attempt to burrow, another kind of labyrinth was devised in which the burrowing instinct might be made use of in escape. While the ocypodas dug their way out in every experiment, they did not usually do so until night.

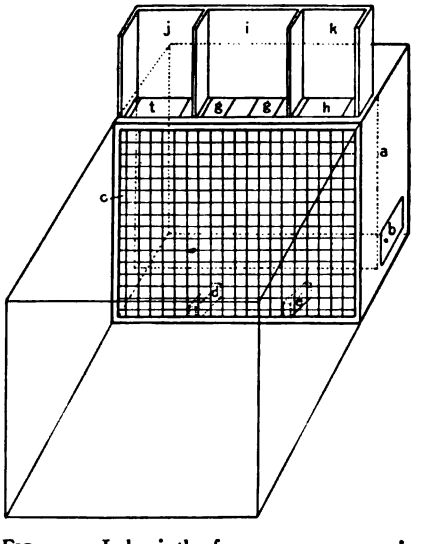

FIG. 10.—Labyrinth for memory experiments.

Having noticed that nearly all individuals were inclined to climb, when confined, another labyrinth was made in which escape might be accomplished by this method. A box 11 inches wide, 15 inches long, and 10.25 inches high was divided lengthways into two equal parts by a vertical wooden partition (*a*) which extended from the top of the box to within 1.5 inches of the floor, thus leaving an opening connecting the two compartments (fig. 10). The

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ocypodas experimented with were introduced into the posterior compartment, shown in fig. 10, through the sliding door indicated (*b*). The front of the box (*c*), instead of being of wood, was made of ordinary fly-screen. At (*d*) and (*e*) on the floor of the box were placed two pieces of wood 2.4 inches long and 1.6 inches high, which divided the anterior compartment into three passageways. In the top of the box at (*f*), (*g*) and (*h*) were set three windows 2.6 inches by 4 inches, made of ordinary window-glass. In the center of the middle window (*g*) an opening was left which was the exit from the labyrinth, and around this window was erected a barrier (*i*) which prevented the crabs from climbing out over the box. Similar ones (*i*) (*k*) were placed around the other windows so as to make the lighting the same in each case. In escaping a crab would have to pass from the posterior compartment into the anterior compartment, climb up the screen, pass through the opening in the middle window, and then climb down the outside of the screen to the surface of the sand in the pen. This pen was inclosed by panes of window-glass, 10 by 15 inches, set vertically.

Six active ocypodas were used in the following tests, but one of these soon died and another was lost, so that in the table below only the time records of four individuals, A, B, C and D, are recorded. As a rule each crab was given two trials a day, and precautions were taken to guard the individuals from disturbing influences of moving objects.

In general there seems to be a decrease in the time required for escape up to the eighth day, but after that the average time increases. This increase may have been due to the condition of the crabs. During the climbing after the eighth day they fell frequently, and this undoubtedly had a bad effect on them.

Time required for escape from labyrinth, recorded in minutes.

Date.	A.	B.	C.	D.	Average.	Date.	A.	B.	C.	D.	Average.
July 6	9	13	3	127	38	July 10	9	18	10	2	9.75
7	4	1.75	65	20	22.68	11	0.25	34	1.5	24	14.93
7	36	14.5	12.5	4	16.75	11	4	8.5	12.5	8.25	8.31
8	21	1	5	19	11.5	12	14.5	17	1.25	23.5	14.06
8	13	6.5	12.5	1	8.25	12	1	3	2.5	16	5.62
8	17.5	15	.5	15	12	13	0.5	7.5	.25	11	4.81
9	2	11.5	.25	6	4.93	13	10.75	41	6.5	49	26.81
9	9	1	6	1.5	4.37	14	5	36	.5	4	11.37
10	10	8	.25	6.5	6.18	15	74	4.5	2.5	.5	20.38
10	46	4	.5	9	14.87	15	3	18	32.5	13	16.62

During the first few experiments the behavior was as follows: Individuals when introduced into the posterior compartment almost invariably ran to the left side; then if active they went into the left passageway and up the screen, usually following the corner of the box quite closely; on arriving at the top they would scratch the left glass window, apparently

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attempting to get out, but failing in this they would either crawl along the edge of the window toward the right until they reached the opening in the middle of the center window, where they would climb out and down into the pen, or they would descend again into the box and after a time repeat the climbing either in the left-hand or right-hand side and occasionally in the middle part of the screen.

Although the time records do not indicate that the ocypodas learned the position of the exit, yet the behavior, after about 5 days, began to indicate that all the individuals had learned it more or less perfectly. They still continued to crawl up along the corners of the box, but they now often climbed across the screen in a diagonal direction toward the exit, from either the right or left passage-way. Toward the end of the series of tests, the ocypodas became quite inactive, often refusing for a long time to move, but when they did become active they frequently climbed almost directly toward the exit.

The fact that in the above labyrinth experiments we do not obtain good quantitative evidence of memory does not show that *Ocypoda* is without memory. It must be admitted that the labyrinth used was a rather difficult one and that the tests did not extend over as long a period as they should. The injury experienced by frequent falls from the screen and the somewhat artificial conditions undoubtedly affected the results.

Another experiment performed shows that *Ocypoda* profits by experience. It had been noticed that individuals in the trap made use of the sea-water given to them in glass dishes in much the same way as individuals under natural conditions use the water in the sea. Accordingly a trap was thoroughly cleaned and stocked with several ocypodas caught in another part of the island. A study of the behavior was then made when a dish of sea-water was put in the trap. Care was taken not to allow any of the water to drop on the sand and the dish was buried until its rim was level with the surface of the sand. The ocypodas apparently did not pay any attention to the dish at first, but after a time, seemingly by chance, they crawled until their legs projected over the edge and into the water. Usually when this occurred to an individual it would settle down, digging the legs of the other side into the sand as it does when waiting for a wave. After a time it often climbed over into the water and moistened its gills. This experiment was repeated for several days, a dish of water being given to them twice a day, and many of the crabs soon went through the same behavior almost as soon as the water was introduced. Finally a dish without water was tried and it was found that some of the crabs behaved in the same manner as when water was in the dish, *i. e.*, they crawled up to its edge, settled as though waiting for a wave, and then finally climbed over into the dry dish.

This behavior I interpret as a case of associative memory, in which the

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crabs formed an association between contact with the glass dish and the presence of water.

In conclusion it may be said that *Ocypoda,* like the crustacea investigated by other workers, has memory, is able to profit by experience, and can form habits.

SUMMARY.

Adult ocypodas build two kinds of burrows. One consists of a single tunnel extending down in the sand for 3 to 4 feet. The other is similar, except that it is shorter and has a passage branching off from it, which is used for escape.

Young ocypodas make short burrows, only a few inches long, which often extend vertically downward.

Breeding in the region of Loggerhead Key probably occurs in the spring and early summer.

Ocypoda is a scavenger and a cannibal. The eyes do not seem to play an important rôle in the detection of food, but they undoubtedly lead individuals to objects which may be food.

That *Ocypoda* is stimulated by odors was not conclusively shown, but certain experiments point strongly in that direction.

The eyes are highly developed, so far as crustacean eyes are concerned; they are quite sensitive to large differences in the intensity of light; they do not react to different colors; they aid much in the search for food, in the detection of enemies, and in the accuracy of locomotion. Ocypodas probably do not have vision such as that of the human eye, nor do they see the color and finer characters of the surface of an object, but they undoubtedly see its outlines and possibly some of the more evident irregularities of the surface made evident by differences in lighting.

The color-pattern seen through the carapace of *Ocypoda* changes in intensity under different conditions of temperaure and light.

In the absence of light when the temperature is anywhere between 22° C. and 45° C., and undoubtedly when it is even lower or higher, a light coloration occurs.

Generally in diffuse light and even direct sunlight a dark coloration appears, provided the temperature is not too high.

Usually at low temperatures, not above 35° C., a dark coloration occurs, provided the eye is stimulated by light.

At high temperatures, above 35° C., a light coloration is the rule, and it occurs independently of the intensity of light.

No indication of audition was observed in *Ocypoda.* The so-called "auditory organs" are equilibrating organs.

Ocypoda has a stridulating ridge on the palm of its large chela. Any sound which it may make is probably not heard by other individuals, but

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the vibrations of sound produced during the movement of this stridulating ridge against the basal joint of the chela are probably felt by other ocypodas.

The tactile sense is well developed in *Ocypoda*. With the body orientated in a fixed position, the animal can move in practically any direction. It runs with a considerable degree of accuracy and undoubtedly has a sense of position and distance. In locomotion these crabs are guided by differences in the lighting of surfaces, by tactile stimuli, by differences in muscular effort and by the stimulation of the equilibrating organs resulting from a tilting of the body.

During most of the time *Ocypoda* lives on land, only going to the water occasionally for the purpose of moistening the gills. When exposed to the direct sunlight without water for more than 4 hours individuals usually die. They can live in their burrows without sea-water for at least 48 hours.

The "Aufbäum Reflex" described by Bethe is an attitude of defense. Ocypoda often hides from man by simply settling down and throwing sand over its body. It is sometimes found in a resting or "sleeping" condition when it does not react to many of the ordinary stimuli. The death-feigning reaction is exhibited under certain conditions.

This brachyuran forms associations and habits.

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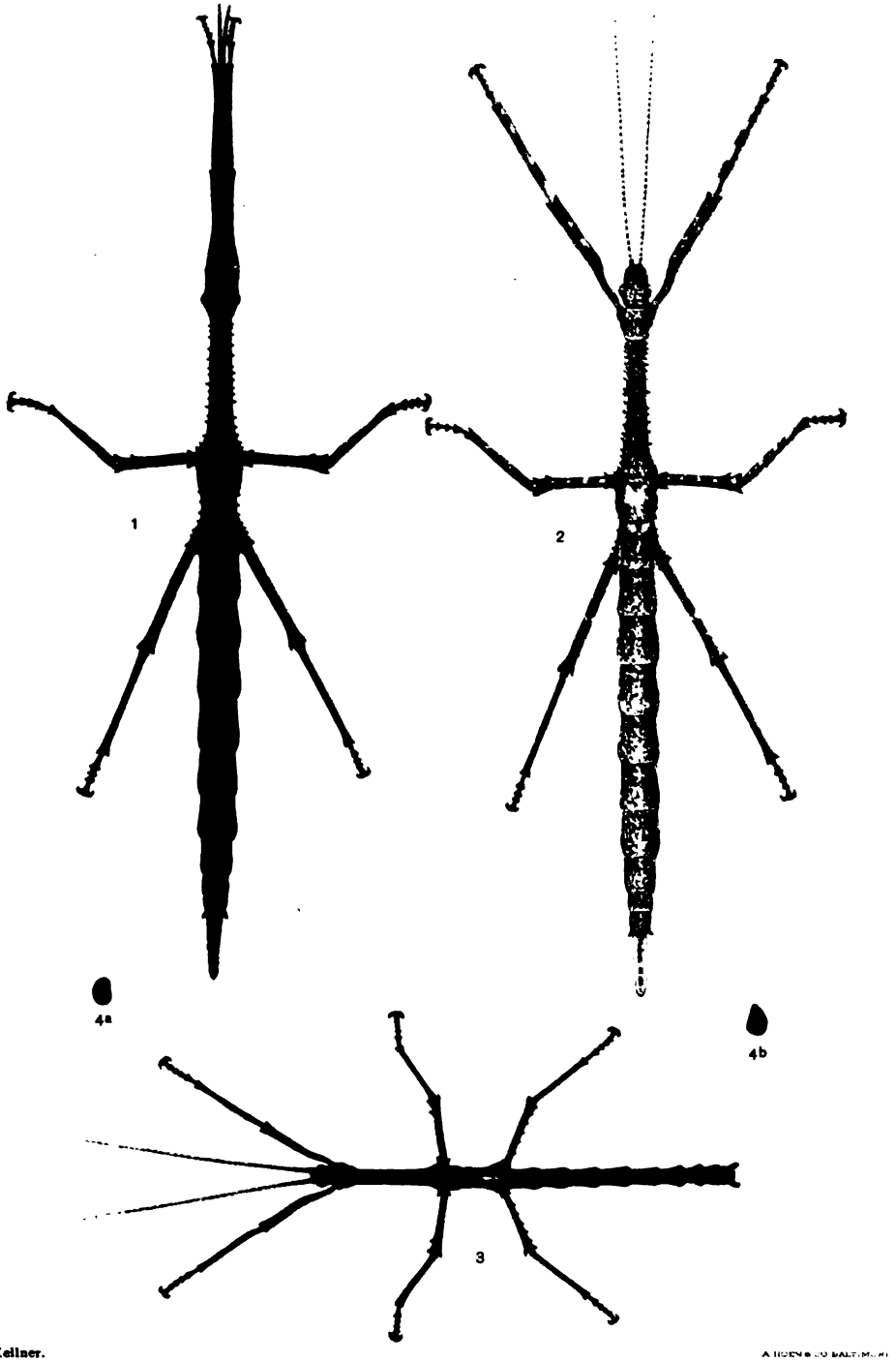

C. Kellner.

Fig. 1. A dark type *Aplopus* female with first pair of legs extending forward, inclosing the antennæ. This position is often assumed and serves to give the anterior end of the insect the appearance of a straight stick.

Fig. 2. The pale-gray type female with first pair of legs apart showing curve in the femora, which fits closely to the head in Fig. 1.

Fig. 3. Male *Aplopus*, indicating his smaller size and green legs. Figs. 1, 2, and 3 are two-thirds natural size.

Fig. 4a. Egg of *Aplopus*, natural size. 4b. Seed of *Suriana maritima*, natural size. The two resemble each other closely in size and color.

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II. HABITS, REACTIONS, AND MATING INSTINCTS OF THE "WALKING STICK," APLOPUS MAYERI.

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3 plates and 1 text figure.

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HABITS, REACTIONS AND MATING INSTINCTS OF THE "WALKING-STICK," APLOPUS MAYERI.

By Charles R. Stockard.

An investigation of the behavior of a protectively adapted insect is important to show definitely whether the actions of such an animal are coordinated with its protective structure. If an insect such as the "walking-stick," which forms the subject of the present discussion, was found to move about briskly on exposed portions of the plant on which it lives, and to show other habits which might attract the attention of enemies in spite of its apparent resemblance to the stems and leafy parts of the plant, then, notwithstanding this resemblance, it would scarcely be as well protected as other insects showing no such resemblance but remaining still and concealed among the leaves and branches of the shrub. It is clear to all observers that the behavior of an animal is almost if not quite as important as its structure in determining whether or not the animal is truly protectively adapted to its surroundings.

With the above as a premise, we may ask what would be the theoretical expectation for protective behavior of such an insect as *Aplopus*. Since movement attracts the attention of birds and other enemies almost or quite as readily as conspicuous appearance, we should first expect this insect to remain perfectly motionless during the day, while it may be seen, and to move at night; in other words, nocturnal habits would be ideal for its protection. *Aplopus* is unable to fly or leap; thus its most effective means of escape would be to drop bodily from a position when touched, and become lost by falling and alighting among the lower branches of the bush, where it might remain motionless and concealed. When moving from place to place it would attract less attention should it move slowly, and the extreme perfection of movement would be to vibrate from side to side as it progressed, as a twig swings in a light breeze. The male is colored with more green than the female; therefore, he may move among the leaves to better advantage and she will be less conspicuous on the larger brown stems. Lastly, since these insects vary greatly in color, as do most protectively colored animals, we might expect, for instance, that light-gray females would rest on the lighter-colored stems, while the dark-brown type would be found on darker stems.

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After studying the habits of the " walking-stick " one finds that the foregoing expectations for its behavior are minutely carried out, with the single exception of the last mentioned.

In the following pages I shall discuss the habits of *Aplopus* and enumerate the results of a number of experiments conducted to test its responses to various stimuli and changed conditions. Record will also be made of some experiments concerning their mating instincts, in which males were induced to copulate with the amputated abdomen of a female attached to a small stick supported by wire legs.

The experiments were performed at the Laboratory of Marine Biology of the Carnegie Institution of Washington, Tortugas, Florida, and it is a pleasure to express my thanks to Dr. Alfred G. Mayer, the Director of the Laboratory, for many courtesies extended to me while there, and for the kindly interest he has shown in my work.

BEHAVIOR OF APLOPUS IN NATURE.

Aplopus mayeri is a large insect, the females often measuring more than 8 inches from the tip of antennæ to the tip of abdomen, while for the smaller male 6 inches is an adult length. The male's antennæ are longer than those of the female. The male is much more sensitive to stimuli and in nature is the more active of the two. Figures 1 and 2 of plate 1 illustrate females and figure 3 shows a male, all reduced to two-thirds natural size. A decided difference in color will be noted between the two females, one being very dark, while the other is a pale gray. A large variety of gradations exist between these two extremes. The males are more or less greenish, but they also vary considerably in color. In some males the abdomen is a rich dark brown, in others a pale drab. The legs in all are darker or lighter shades of green. Such variations are common within the family Phasmidæ, all members of which are more or less protectively colored and constructed.

The young males are brown or grayish, resembling the females in color, and can only be distinguished from them by the absence of the oviscapt and the presence of a prominent organ of intromission on their ventral surfaces near the tip of the abdomen. At maturity, however, the males acquire the adult greenish color and may then be recognized at a glance. The wings of both sexes are rudimentary, but are capable of being raised when the animal is greatly excited, giving to it a lively and agitated appearance. *Aplopus* has spines and prominences on its body and legs suggesting the slight irregularities on the bark of twigs.

These insects are found only on their food-plant, *Suriana maritima,* and on this shrub they are extremely difficult to detect. In color and shape the female resembles closely the stems of small branches. The greenish color of the male conceals it among the leaves, while one may find a close resemblance in size and color between the eggs of *Aplopus* and the seed of

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Suriana, both of which fall from the branches to the ground, where they are obscured among the débris (figs. 4*a* and 4*b* of plate 1).

The "walking-sticks" are not easily collected during the day, though at night, when they become active, one may obtain them in large numbers by means of a lantern. The following instance may be cited as illustrating the extent to which these insects are concealed as they sit among the branches. A small group of bushes about 10 feet in diameter contained six large females and two adult males. Three of the females were sitting near the edge of the bushes and within about 2 feet of one another. A person unaccustomed to searching for the insects, although familiar with their appearance, attempted to find the three, but failed to locate any of them. I then followed after him and succeeded in locating two, but failed to find the third until a second careful search was made.

As a test of how readily birds might find aplopi while in their motionless attitude, five individuals were placed on the ground near a hen with several small chickens. The mother showed no evidence of recognizing the insects until within a short time the *Aplopi* became excited at finding themselves on the ground and began to crawl toward a bush. When they began moving the hen immediately started after them.

The observations and experiments that follow were based on the actions of 26 males and 81 females, some of which were kept in cages, while others were allowed to remain in their natural environment on isolated *Suriana* bushes.

ATTITUDES WHEN AT REST.

Aplopus assumes a decidedly protective attitude when at rest. The forelegs, which are slightly grooved on their anterior surfaces, are directed forward, the grooves being approximated to form a tube inclosing the antennæ, thus producing a resemblance between the anterior end of the animal and the straight end of a small dead stick (see fig. 1 of plate 1 and also figs. 1, 2, and 3 of plate 2, photographs from life of the insects in such a position). With their forelegs straightened in this manner, the females usually rest in an obliquely vertical position on the leafless stems. The abdomen sometimes points upward, the tips of the forelimbs being directed down, grasping the branch on which they rest. Again, the abdomen may be turned downward and serve as a partial support, while the body, with the extended forelegs free, points obliquely upward. In either attitude the insect closely simulates a dead stick projecting from the supporting branch. The femora of the first pair of legs are curved near their proximal joints so as to fit closely around the insect's head when they are extended forward (fig. 2 of plate 1). The females, as mentioned before, vary considerably in color from dark brown to light gray, as do also the stems of *Suriana,* though the insects do not at all times take advantage of this variation, the dark females being not uncommonly seen on light stems, and *vice versa.*

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The males do not so constantly assume the position with the first legs extended. This attitude is less essential for them than for the females, since they are found as a rule among the leafed branches, where their greenish legs are inconspicuous. Their slenderer proportions and smaller size also make them more difficult to see. At times, however, the males do straighten their first pair of legs forward and assume the position so common to the female.

The more common occurrence of the greenish males among the foliage and of the brown females upon the brown stems of the plant suggest the case of *Mantis religiosa*. Di Cesnola[1] records this mantis as occurring in a green and a brown form in Italy, the green form being always found upon green grass and the brown form upon grass burnt by the sun. He found that when 25 individuals of the green form were tied on brown grass all were killed in 11 days, while 20 tied on green grass were all alive after 17 days. The results were similar when the brown form was tied on green and burnt grass.

MOVEMENTS OF APLOPUS.

Aplopus is nocturnal in its habits. During the day it sits motionless among the branches, but as the sun's rays weaken the males begin to move about first, and later the females. Their manner of walking is peculiarly interesting. They resemble sticks crawling about on legs. The legs are moved in a stiff manner and the insect progresses slowly as a rule, although they sometimes move at a rapid gait. While walking among the branches or on a flat surface they often show a lateral swinging movement, the foothold forming a fixed point, while by bending the tarsal and knee joints the body is swung sidewise, sometimes with an amplitude of more than half an inch. This movement suggests to the observer the swinging or waving motion of branches and stems when shaken, or blown by the wind. The male has also a peculiar quivering movement that is sometimes performed at intervals while moving about the branches. This motion is more to be associated with the mating instincts, as is shown below. In the evening *Aplopus* shows a tendency to climb upward, being negatively geotropic. It will then often turn and go upward if the twig is inverted after it has reached the top.

The males travel greater distances during the night than do the females. Three females under observation did not move more than 2 feet from their original positions within a period of two days, yet others were found to migrate to parts of the bushes 10 or 12 feet distant during a single night. The males usually travel many yards in a night and it is almost impossible to keep track of them for more than one day.

Aplopus avoids or escapes its enemies in the following ways: On several

[1] Di Cesnola, A. P. Preliminary note on the protective value of color in *Mantis religiosa*. Biometrika, III, p. 58, 1904.

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Fig. 1. Female Aplopus in normal attitude on Suriana branch.

Fig. 2. Female in somewhat different position.

Fig. 3. Light-gray female on a dark stem of Suriana.

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occasions females were touched lightly as they sat in their protective attitude. They remained motionless after being touched, as though they were inanimate bodies. A male under observation about dusk was struck by a large insect which flew against it; the *Aplopus* jerked quickly back and remained motionless for more than a minute, after which it walked swiftly down the branch.

The most effective means of escape for these animals is the "dropping reaction." When one attempting to capture an *Aplopus* fails to seize it the first time, it often drops bodily from the limb on which it rested and catches on some lower branch that it may chance to strike. If seen and unsuccessfully grabbed at for the second time, it will again drop and may sometimes fall entirely to the ground. One male in attempting to escape capture fell to the ground, striking on its back with its legs extended in the air. It feigned death perfectly and remained in this awkward position for more than 8 minutes; then turned itself over and moved away so quickly that it was lost sight of in the dim evening light.

Since "walking-sticks" are unable either to fly or jump, this dropping reaction is a most important means of escape, and the dense growth of the *Suriana* bushes would apparently prevent birds from finding the insect a second time after it had so suddenly fallen out of reach. Their motionless attitudes during the day and close resemblance to the stems of the bushes no doubt serve to protect *Aplopus* to a marked degree from predaceous birds and other enemies.

The food of *Aplopus* consists entirely of the leaves of *Suriana maritima*, the plant on which it lives. The only previously published statement regarding its habits is a brief paragraph in the catalogue from the supply department of the Marine Biological Laboratory at Woods Hole. This states that "the prey is seized by a quick movement of the forelegs." Such an idea is, of course, erroneous, since all members of this family are known to be vegetable feeders. The statement is doubtless based on the opinion of some amateur collector. *Aplopus* usually feeds at night, although those resting on leafy branches are sometimes observed to feed during the day. In feeding they bite the leaf straight across the top and often eat it entirely away, or they may bite the leaf in an up-and-down fashion until it is consumed. They rarely make semicircular cuts in the leaves, as the locust often does. These characteristically bitten leaves serve to furnish a trustworthy index of the whereabouts of *Aplopi*, as they seem to be somewhat locally distributed on the island.

MATING INSTINCTS.

Mating occurs as a rule during the night, although several pairs were observed *in copulo* during the day. The active process is much the same as in kindred insects. The male takes a position on the back of the female, with his front feet resting on her metathorax, the second pair of feet

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grasping her abdomen about its middle, his third pair of legs usually hanging freely extended, the tip of his abdomen being firmly attached to a slight pit on the ventral surface of the seventh abdominal segment of the female. The intromissive organ of the male is then protruded and placed between the oviscapt and the last three abdominal segments of the female. In this position the male remains for from 30 minutes to several hours. His copulating organ is then withdrawn, although he may still remain for a long time sitting upon the back of the female (fig. 4, plate 3). One male may copulate with several females during the same day. The male often gives periodical quivering movements while over the female, probably for the purpose of exciting her to the sexual act. He sometimes shows a slow, swinging motion during copulation.

The female is supplied with a long ovipositor, although it seems to be useless, as her eggs are allowed to fall carelessly to the ground as she sits motionless among the branches. The eggs resemble closely in size and color the seed of *Suriana,* as mentioned before, but differ from them considerably in shape. (Compare figs. *4a* and *4b* in plate 1.)

All of the observations on the habits of *Aplopus* in nature would seem to indicate that the behavior of this insect is as truly protective as is its close simulation of the branches on which it lives.

EXPERIMENTAL.

EXPERIMENTS WITH LIGHT.

Aplopus responds to light and darkness in a most interesting manner. The insects were observed to begin moving on the bushes by a much brighter light in the evening than that which served to stop their movement during the morning. They were seen feeding and crawling slowly about, at times, two hours before sunset; while they often came to rest more than half an hour before sunrise. The difference in intensities of the lights causing the two reactions is very great. It occurred to me that perhaps their response was periodic and not entirely due to the effect of light; that is, after being active for several hours during the night they become tired and cease to move for this reason, and not on account of any response to light, since the intensity of the morning light by which they come to rest is even less than that of the moonlight in which they are active. (The quality of the two lights is no doubt different.) The case is, however, made clear by the following experiment:

Sixty-five individuals in a wire cage had come to rest at $4^h\ 50^m$ a. m. At this time daylight was scarcely perceptible. It was much darker than when they had begun movement during the evening, or even the moonlight of the earlier part of the night. It would seem, then, that a physiological periodicity had had some influence on their behavior. To test this the cage was placed in a dark-room at 5 a. m. In less than half an hour all were

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actively crawling, thus showing that they had responded to the faint light of approaching day and not to a tired condition. They continued to move actively for more than an hour in the dark-room, and were then put into the light, where they readily came to rest again.

The fact that they begin movement by brighter light in the evening and stop by paler or weaker light in the morning may possibly be associated with a similar habit of some birds, which go to their roosts by brighter light than that by which they leave.

A number of dark-room experiments were performed during the day to test the manner and time of response to light and darkness. The dark-room was one arranged for photographic work, having a red glass window that might be covered with a black oilcloth, so that no light was admitted. The door of the room opened into the closed side of the laboratory, thus permitting only weak diffused light to enter the room at any time. I was enabled to detect the first movement of the insects in the dark, as the gauze wire of the cage gave a perceptible clicking sound when their feet were moved upon it.

We may first consider the reactions of normal individuals. Since the experiments gave closely similar results, one may be recorded for illustration. Three females and two males were placed in the dark-room at $10^h\ 25^m$ a. m. After 15 minutes three were actively moving, while after 20 minutes all were in motion. The door was opened and light admitted at 11 a. m.; they came to rest in a little more than a minute, and remained so in spite of various loud noises until $11^h\ 11^m$ a. m., when the room was again darkened. The animals began again to move and all five were in active motion within 8 minutes. Bright daylight was thrown on them after all had been moving for 3 minutes; two were at rest in less than a minute, and all were quiet in about 2 minutes. When they had been at rest for 5 minutes the room was for the third time darkened, and after 11 minutes all were active. Light was then admitted and two ceased to move within 2 minutes, the others stopping after 5 minutes.

The dark-room was again closed at $11^h\ 45^m$ a. m. and left until $12^h\ 30^m$ p. m., at which time all of the insects were active. On admitting light they became motionless within 2 minutes. The dark-room was closed for the fifth time at $12^h\ 55^m$ p. m., after the five "walking-sticks" had been quiet for more than 20 minutes; 10 minutes after they had been in the dark two were moving, and all were in motion after 15 minutes or at $1^h\ 10^m$ p. m. Light was admitted at $1^h\ 11^m$ p. m., and all came to rest within 30 seconds, a very quick response. They were then exposed to light for 10 minutes, then again put into the dark-room. The first one did not begin to move until 17 minutes had elapsed; the others were moving after being in the dark 20 minutes. The first ones to move had disturbed others by striking against them, so that these probably moved earlier than they would have otherwise.

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They were allowed to remain active for 10 minutes and were then placed in bright light, where they again stopped all movement in less than 30 seconds. They were observed closely for 10 minutes while in the light, and not a leg or antenna was moved, though some had stopped in apparently awkward positions.

The foregoing experiment was repeated several times on different individuals and at various periods during the day, always giving similar results. *Aplopus* is thus seen to become active in the dark within from 10 to 20 minutes, and at times even more promptly. This activity is continued as long as it remains in the dark. When the insect is placed in bright light it promptly comes to rest within from less than 30 seconds in some cases to several minutes in others. *Aplopus* responds, therefore, more promptly to light than to darkness. The males appear to come to rest more readily than the females; they are also more active in the dark. These insects may readily be made to mate by placing a number of individuals of both sexes in a cage in the dark.

The question next arises whether responses to light and darkness are due to the action of the stimulus on the optic organs or to the effects of light on the body-surface of the insect as a whole. In attempting an answer to this question several experiments were performed. First, a number of *Aplopi* were chosen and their eyes were well covered with a lampblack paste until they were apparently blind. These individuals were then subjected to dark-room experiments. When only the compound eyes were blackened, the simple eyes being uncovered, they still responded in the dark-room, though slower than the control. On one occasion a male and three females were used; the male moved slightly after 15 minutes, though almost an hour had elapsed before all four individuals had become active.

When both the simple and compound eyes were blackened they responded still more slowly in the dark. Of four treated in this manner only one had moved after 30 minutes in the dark-room, and this one almost immediately came to rest again; so that after 50 minutes all were quiet, three of the four not having moved during this time. After 2 hours three were at rest and one was moving; one of the four had not moved at all during the two hours and the three that had moved did so only for a moment, not becoming really active, as they normally do in the dark-room.

To test further the importance of vision in responding to changes from light to dark, I determined to blacken the compound and simple eyes of a number of *Aplopi* during the night to ascertain in what manner they would respond when the daylight appeared. Six females and two males were placed in a cage to themselves and their eyes were painted at 9^h 40^m p. m., while they were all very active. At 5^h 30^m a. m. on the following morning three of the females and one of the males were actively moving. These animals were much more active than the control of about 50 individuals, all

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of which were now at rest, although they were caged nearby so as to experience the same light conditions. At 6 o'clock four of the blind ones were still active, although the sun had been shining for half an hour. At 8 o'clock all were at rest, yet they were more than an hour later than the control in responding to the morning light. When these blind insects had been at rest for 2 hours they were placed in the dark-room, where all became active after about an hour. They were then brought into the light and assumed the attitude of rest within 12 minutes.

In the evening the ones with painted eyes became active 30 to 45 minutes earlier than the normal ones did. At 6^h 12^m p. m. not one of 50 normal insects had moved, while 5 of the 8 blind ones had been moving actively for 40 minutes. *Aplopi* probably appreciate light to some extent through their bodies, but more acutely by means of their eyes; thus night appears to come earlier and day later to the blind ones. The 2 blind males failed to pair with either of the 6 blind females, though normal males and females usually mated when they were caged together.

Blind and normal females were observed in their natural environment on *Suriana* bushes. Here the blind individuals also became active earlier in the evening than the normal ones.

When the strong light of a bull's-eye lantern is thrown on a normal one of these insects at night, it turns its head from side to side and gives evidence of seeing the light.

These experiments seem to show that *Aplopus* may respond to light and darkness through its general body surfaces, but that it does so much less readily, or slower, than by means of its optic organs.

EXPERIMENTS WITH LIGHT RAYS OF DIFFERENT LENGTHS.

It became desirable at this stage to know whether the insects responded to white light as a complex whole or to some of its constituent rays. Several experiments were conducted in the attempt to solve this problem.

Light was passed through a vessel containing carbon bisulphide, which serves to eliminate the ultra-violet rays. This is the well-known experiment first performed by Sir John Lubbock on ants. A dark-jar was arranged and two of the "walking-sticks" were placed in it. After they had been quiet for 10 minutes the jar was covered by a vessel containing sea-water in order to test the effect of the subdued light which was transmitted by the liquid. The animals under this condition remained motionless for 25 minutes. The vessel containing the sea-water was then removed, and the jar allowed to stand uncovered for 10 minutes. The insects still retained their daylight state of rest. A vessel containing carbon bisulphide was now placed over the jar, thus admitting daylight minus its ultra-violet rays. The *Aplopi* remained perfectly motionless in this light for 85 minutes and were then removed from the jar. It thus seems apparent that this insect is not

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brought to rest by the ultra-violet rays of sunlight, since they do not move in the absence of such rays. They probably respond, therefore, to the visible rays of the spectrum.

Ten *Aplopi* were subjected to light transmitted through blue glass. (Spectroscopic analysis showed this glass to be impure, transmitting blue, green, and a little red and yellow.) The insects gave no definite response in this light, although during one experiment they became more active than usual, moving as if they were in the dark. Such a response was, however, not at all constant and I am inclined to think that the individuals of this experiment had become unduly excited from some other cause.

The influence of red light, containing possibly a little orange, was tried on ten *Aplopi*. This also failed to give any definite reaction. It seems likely, then, that these insects respond to sunlight as a complex light and not to a limited number of its rays—at any rate not to the few tested above.

EXPERIMENTS WITH SOUND.

Aplopus seems indifferent to loud noises; a loud voice or a strong rap upon a board is apparently unheard. A 32-caliber pistol was fired three times within 18 inches of three active individuals, one male and two females, yet they gave no indication of having heard the pistol. Before the pistol was fired the second time the "walking-sticks" were made to assume awkward positions; still they remained motionless after the noise.

MOVEMENT EXPERIMENTS.

Aplopus may be made to assume almost any position, it matters not how apparently awkward, and it will often retain such a position for a long period of time. Such a response may be very useful in causing this animal to be passed unnoticed. If it be shaken or struck while resting on a limb it will not at first scamper off as most insects would, but remains perfectly still in almost any position it may chance to occupy after the shock. When such a disturbance is repeated for several times, *Aplopus* may become excited and either drop or attempt to run away. One of either pair of legs may be lifted from its foothold and be straightened or twisted backward or forward and left with the foot free and unsupported. The leg may remain motionless in such a position for long periods of time. Two or even three legs can be raised in such a fashion, and *Aplopus* will stand motionless on its remaining foothold. Not more than three of its feet can be raised at any one time, since it is unable to support its long body upon only two legs. The antennæ may be directed in any direction the observer may wish and the insect will permit them to remain in such a position. One may actually lift an unexcited *Aplopus* by its long mesothorax and slowly place it back down upon a flat surface, where it will remain for 10 minutes or more with its legs pointing upward. A second individual may be placed in a similar manner over the first, and both will remain motionless for many minutes. As mentioned above, they show a death-feigning reaction.

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This insect suggests to one a papier-maché imitation with wire legs which may be bent or twisted in almost any manner and put in any position. It could scarcely be more stick-like.

When walking, *Aplopus* often stops and waves its antennæ about in a circle, apparently feeling for some object in front of it. If the antennæ strike an object, a stick or a leaf, the first pair of legs reach forward and attempt to grasp it and pull the body of the insect up to it. When the insects have climbed to the top of a branch they usually wave their antennæ, trying to find some object on which to continue their upward journey. The antennæ of several individuals were cut away close to their proximal joints. The insects were slightly excited by the operation, but soon moved off, using their first pair of legs as feelers, stopping at intervals and waving either the right or left leg and at times circling both legs in front of the head, just as if the legs were efficient antennæ. One of the first pair of legs was removed, and the remaining one then served the purpose of a feeler. The other first leg was then removed, leaving the animal without antennæ or either first leg. The insect now progressed in a slower but surprisingly normal fashion upon only four legs. The point of especial interest is that first the one and then the other of the second pair of legs was raised and circled about as an antenna or feeler. Both of these legs could not be so used at any one time, since the insect is unable to stand on less than three legs. Normal insects were never observed to use either of the second pair of legs as feelers.

The eyes of such a four-legged, antennaless animal were blackened so that it was unable to see. This confused the subject considerably and it turned several times in a circle before being able to progress straight forward. The progress was then slow and cautious. Such an *Aplopus* often turned its head from side to side, as if attempting to see; it also moved the stumps of its antennæ and legs. It was able to climb among the branches and feed in a typical manner. On the following day it showed marked improvement in its ability to progress. When at rest these crippled individuals directed the remaining proximal portions of their antennæ and first legs forward, just as though they were assuming the attitude with legs and antennæ pointing straight out in front of the head, which is so typical for normal individuals.

A strong electric current causes *Aplopus* to move actively and may often cause its legs to kick violently for some seconds.

MATING OF MALES WITH A PORTION OF A FEMALE ABDOMEN ATTACHED TO A STICK.

Many experimenters have attempted in various ways to determine through what senses the male insect locates and mates with the female. Among the moths and butterflies the sexes are sometimes differently colored

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and observers have claimed that the adornment of the male or of the female was a factor in the selection of the other sex. This manner of viewing the case was seriously questioned by some interesting experiments performed by Mayer in 1900.[1] A number of female moths were placed in an open-mouth glass jar covered by netting and five males when liberated 100 feet away flew to the jar. The experiment was then repeated with the jar inverted, so as to close the opening. This time the males did not approach, although the females were visible through the glass. It thus appears that the male moth finds the female by the sense of smell rather than the sense of sight. Other females were inclosed in a box with an open chimney, and the males flew to the chimney, although the females were not visible. When abdomens of females were cut off, the males would fly to these rather than to the winged bodies. If the antennæ of the male be removed he does not go to the female.

Mayer also glued the wings of a male over the wings of a female, so that she appeared like a male; nevertheless she was found by a male and mated with normally. Males would pay no attention to other males with female wings, but would pair readily with a female both of whose wings had been cut away.

In all of these experiments, however, the male and female were in healthy conditions during mating, so that they were capable of movement or actions by which the sexes might excite one another. Dr. Mayer informs me that during his experience a male would not mate with a fatally mutilated or dying female.

I wished to conduct an experiment that would eliminate the possibility of anything like a courtship or psychical action between the sexes. Since it seems to be the odor of the abdomen of the female that first attracts the male, I concluded to make papier-maché imitation females and smear the abdomen of these with juices from the abdomen of mature females; then, on caging a number of males with these imitation females, pairing might take place. The papier-maché imitations could not be obtained, however, so this experiment was abandoned, though it is probably well worth trying with a number of insects.

It was then decided to construct an artificial female by fastening a portion of the abdomen of a mature female *Aplopus* on to a small stick. A *Suriana* stick was cut that approximated in thickness the female's body and supported on six wire legs. One end of the stick was trimmed to a conical point and the abdomen of a female minus the first segment was pushed on over this conical end and made fast by winding thread about it. An abdomen thus attached to a stick will remain alive and is capable of moving slightly, and indeed defecating after more than 24 hours. The head and

[1] Mayer, A. G. On the mating instinct in moths. Annal. and Mag. Nat. History, v, 1900.

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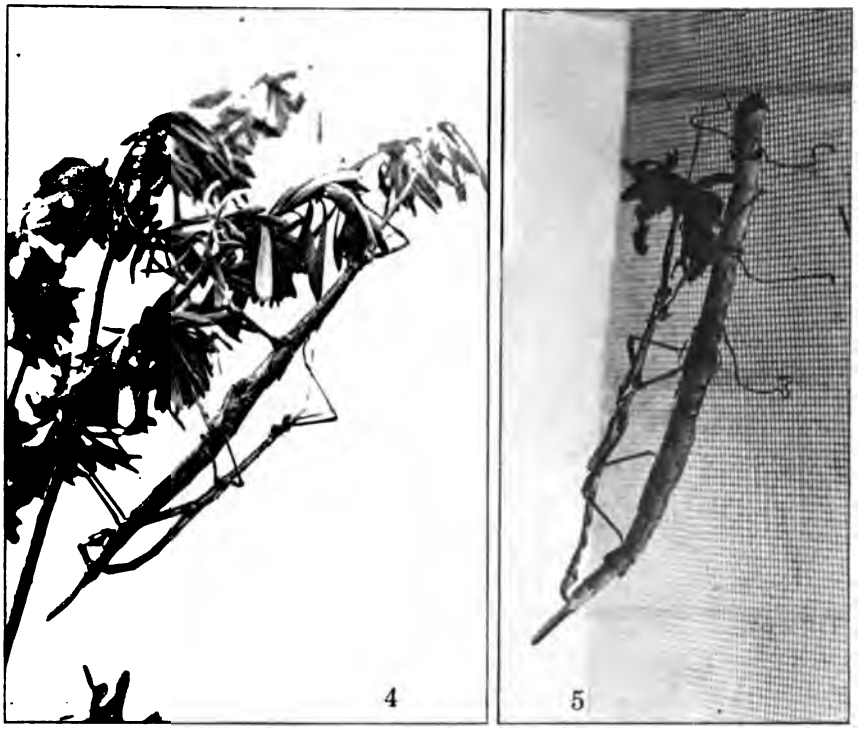

Fig. 4. A mating pair of Aplopi. The male has withdrawn his intromission organ but still grasps abdomen of female.

Fig. 5. Male Aplopus immediately after he has withdrawn his intromission organ while copulating with the amputated abdomen of a female fixed to a wire-legged stick.

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thorax also continue to live and crawl about in the usual manner for several days after the abdomen has been removed.

I induced two male aplopi to pair with such a "stick-female" in a perfectly normal manner (text-fig. 1 and plate 3, fig. 5). The experiment was performed as follows: It had been found, if a male was separated from a normal female while mating with her, that they would remate after a short time if placed in the dark. It had also been found by a previous unsuccessful experiment that the abdomen should be from a female that was mature, but that had not been mated with. This in mind, five males and ten females were put into a dark-room, where after 12 minutes one of the males had paired with a female. The pair was separated and the abdomen of the female cut off at the joint between the first and second segments and fixed

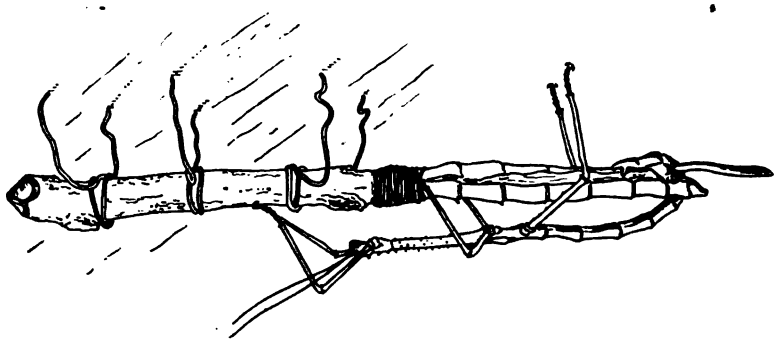

FIG. 1.—Drawing of male *Aplopus* in full copulating attitude with the end of a female abdomen fixed to a wire-legged stick.

to the stick with wire legs as described above. All of the females were now removed from the cage and the abdomen on the wire-legged stick was attached to the side of the cage in a vertical position and placed in the dark-room with four males.

After 1.5 hours the "stick-female" had not been disturbed by any of the males. It was now moved and placed in a horizontal position, as if holding to the gauze-wire top of the cage by its legs, with its body suspended, the attitude of any insect while clinging to the under side of a horizontal surface (fig. 1). *In such a position the abdomen was mated with in less than an hour.* The male in this instance was not the same individual that had previously mated with the entire female. He was in a perfectly normal copulating attitude, his organ of intromission being inserted between the oviscapt and the raised end of the female abdomen, as is shown in figure 1. Figure 5, plate 3, is a photograph of the pair, although here the male has withdrawn his intromissive organ on account of the disturbance caused by shifting the cage into a favorable light for photographing. This male was finally, by the movements of the cage, made to leave the "stick-female."

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A point of some interest is that *Aplopus* seems to prefer the female to occupy a horizontal position in mating. During the first experiment with the "stick-female" it was placed in a vertical position and caged with males in the dark for two days without a result. In the experiment above the "stick-female" was first placed vertically and remained so for 1.5 hours without attracting a male. When it was changed to a horizontal position a male paired with it in less than an hour. All of the normal pairs observed were in a more or less horizontal position. It may be that the attitudes of the male are difficult to assume unless the female stands horizontally.

The cage with the "stick-female" and four males was again returned to the dark-room and after 2.5 hours a second male was found standing on the decoy. He remained in this position for over 3 hours, which was a much longer time than I had known a male to stand over a normal female without copulating with her. After this time, however, he began the usual mating movements and copulated perfectly with the abdomen. This was, then, the second time that the amputated abdomen of the female had been paired with, and each time by a different male. No doubt, therefore, remains that the male *Aplopus* may pair normally with the female without any "communication," "courtship," or psychical processes having taken place between them.

SUMMARY AND CONCLUSIONS.

1. The habits of *Aplopus mayeri* on its food-plant *Suriana maritima* are as truly protectively adapted as is its singular stick-like appearance. The large females in their color and shape resemble the stem of this plant; the males are greenish and well concealed among the leafed twigs, while the eggs are peculiarly similar to the seeds of *Suriana* in size and color, although differing in shape. The insect is nocturnal and only occasionally moves in the daylight; then as a rule with a slow, waving motion suggesting the movement of a branch swinging in a light breeze. To escape enemies it may fall bodily from its position and become lost among the lower branches of the shrub, or at times it may fall entirely to the ground, where it will lie motionless for several minutes as if feigning death.

2. *Aplopus* becomes active by a much brighter light in the evening than that by which it comes to rest in the morning. Both reactions are, however, responses to light and not to a physiological periodicity, as may be shown with dark-room experiments. If these insects are blinded by painting their eyes with lampblack paste, they still respond to light and darkness, although much slower than normally.

3. They gave no response to sunlight lacking the ultra-violet rays, and were equally indifferent to red and blue lights, acting in all as though they were in ordinary daylight.

4. *Aplopus* gives no indication of hearing sounds of various intensities.

5. These insects during the day, while inactive, may be made to assume

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an almost endless variety of positions, any of which they will maintain for a considerable period of time. They may actually be piled over one another, with their backs down and legs extended in the air, as if they were inanimate sticks. Such stick-like indifference may often assist them to pass unnoticed by enemies that might otherwise be attracted by their movements.

6. While moving about, the antennæ are often waved or circled in front of their heads, as if feeling the way. Should the antennæ be removed, the forelegs are readily pressed into service as feelers, these being waved much as if they were true antennæ. If now the first pair of legs are removed it is interesting to find that the legs of the second pair are alternately waved about and used as feelers, although normal insects were never seen to use either leg of the second pair in such a manner. *Aplopus,* considering the length of its body, progresses remarkably well with only four legs. If such a four-legged, antennaless individual has its eyes blinded, it becomes much confused and often turns in a circle, and twists its head from side to side as it walks. It improves in its movements with practice.

7. The abdomen of a mature female was cut off between the first and second segments and tied to a stick which was supported on wire legs. Males in a dark-room were found to copulate in a normal manner with this amputated female abdomen fastened on the stick. This is a unique case of a male insect's pairing with a removed portion of the female. Such an experiment makes it evident that a courtship or psychical response is not essential between the two sexes in mating.

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III. STUDIES OF TISSUE GROWTH.

1. AN EXPERIMENTAL STUDY OF THE RATE OF REGENERATION IN CASSIOPEA XAMACHANA (BIGELOW).

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29 text figures.

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AN EXPERIMENTAL STUDY OF THE RATE OF REGENERATION IN CASSIOPEA XAMACHANA (BIGELOW).

By Charles R. Stockard.

INTRODUCTION.

The suggestion has been advanced by Zeleny (1903 and 1905) that the greater the degree of injury, up to a certain limit, the more rapid will be the rate of regeneration. Zeleny's studies were based on the regeneration of the limbs in crustacea and the arms of the brittle-star, *Ophioglypha*. He was unable to offer any satisfactory explanation of why the regeneration rate increased with the amount of injury, but advanced several suggestive hypotheses which are subject to experimental test. First, he pointed out that the animal with the greater number of appendages removed might exercise the regenerating ones more vigorously than does the animal with the smaller number removed. In other words, activity should increase the rate of regeneration in animals. Child (1904) had also been led to think that some regulating influence was exerted over regenerating tissue by movement and nerve impulses in the flat-worm, *Leptoplana*. I have succeeded in devising two different ways of testing the influence of rest and activity on the regenerating tissues of the medusa and find no increase in the rate of regeneration to result from activity.

It was also suggested that the amount of available food might regulate the rate of regeneration. Those crayfish most injured have more food to draw from, since the other appendages are not present to take their share of it. Morgan (1906) has subjected this question to thorough investigation and finds that the amount or rate of differentiation of the regenerating organ is independent of the food supply, although the size of the organ is greater in well-fed individuals than in starved ones. "So long as there is enough food material in the blood or other fluids of the body to allow growth to take place at all it goes on at a rate determined by the peculiarities of each level, and largely independent of the food supply." Here Morgan mentions one of the most interesting points connected with this subject—that is, the influence of different levels of the body, or of an organ, on the rate of regeneration. In the fish's caudal fin it was found that new tissues regenerated faster the nearer the cut was to the base of the fin, and slower the nearer

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the cut to the free end of the fin. At first thought this statement seems only a different way of saying, "the greater the amount of injury the more rapid will be the rate of regeneration." This is not true, however, as it was shown that the rate of regeneration varied with the shape of the cut in a manner not always correlated with the extent of the injury. Experiments will be recorded in the present paper which seem to contrast the two factors distinctly, as well as to show the peculiar influence of the level at which the cut is made.

Again, Zeleny offers the interesting conjecture that the uninjured chelæ may be assumed to exert a retarding influence upon the growth or regeneration of all the others. When one chela is removed the number of uninjured limbs remaining is greater than when both chelæ and the last two pairs of walking-legs are removed. The retarding influence with one chela gone, if the supposition be true, is greater than it is when more limbs are removed and correspondingly the rate of regeneration in the former is slower than in the latter case. Such an explanation when modified might be applied to regeneration in the salamander, the fish, and the medusa in the following way: When these animals are cut at various levels they regenerate faster the farther the cut surface, within certain limits of course, is from the extremity or limits of the animal's body. A fish's tail-fin grows faster from a straight cut near the base than from a similar cut near the end of the fin. The medusa regenerates tissue faster the farther away from the periphery the cut is made, as though the more tissue removed the less uninjured body-surface remained to exert a retarding influence.

The above considerations suggest the question of the limits of growth; as the body nears its adult or normal size the rate of growth becomes slower. It is also true that the regenerating tissue grows slower as it reaches the limits of the former body-surface. Morgan (1906) has expressed this idea as follows:

> If we can find the explanation for the cessation of growth at the proper terminus we can probably find also an explanation for the difference in the rate at different levels, for, as can be shown, the two things appear to be one and the same. In other words, as the new part grows larger its materials change, and this change is of such a kind that it leads to the cessation of growth. Hence starting under different conditions at different levels the same end result will be reached in all cases, and when the terminus is reached the growth should slowly decline, as we find in fact that it does.

Emmel (1906 and 1907) has arrived at opposite conclusions after a study of regeneration and molting in the lobster from those cited above as obtained by Zeleny on the crayfish. Scott (1907), from a study of regeneration on the fins of *Fundulus,* reaches conclusions differing both from those of Zeleny and Emmel as well, since he finds that the degree of injury exerts no influence whatever over the rate of regeneration in the fish's fin. Be this as it may, the fact remains that in the salamander, the fish, the earthworm,

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and the medusa the rate of regeneration does vary under various conditions of injury, but depends upon the body-level at which the cut is made.

The crustacea seem rather unsatisfactory forms for the study of such problems as the rate of regeneration. They must molt before the regenerating portion can be observed and the time between molts is often greater than the time which would be expected as necessary for the given amount of regeneration to take place. There is likely a period of cessation of regenerative growth preceding each molt. Animals which have a continuous growth of regenerating tissue seem much better adapted to these studies.

The experiments here recorded were conducted in the Laboratory of Marine Biology of the Carnegie Institution of Washington, at Dry Tortugas, Florida, during the summer of 1907. I wish to express my thanks to the Director of the Laboratory, Dr. Alfred G. Mayer, for many kindnesses extended me while there.

MATERIAL.

The rhizostomous scyphomedusa *Cassiopea xamachana* is very hardy. It attains a large size, 15 or 20 cm. in diameter, and is particularly suited to regeneration studies, as several experiments or cuts may be performed on one and the same individual where the conditions are as near similar as would be possible to obtain. Further, since all portions of the disk seem capable of regeneration one may thus work on the animal's body as well as on its tentacle-like appendages. Of exceptional importance is the fact that the circular disk will admit of variously patterned cuts which are impossible on animals with a differently shaped body. Finally, the disk pulsates rhythmically in a manner subject to the control of the experimenter, thus enabling him to test the influence of motion, or activity, on the regenerating tissue in a way not offered by any other animal yet experimented upon.

These medusæ are easily kept for long periods of time in small aquaria by merely changing the water every two or three days. They live for some time without taking food. One may collect them in abundance from the moat which surrounds the old Fort Jefferson at the Tortugas Islands. The water in this moat is about 4 to 6 feet deep, being rather stagnant at times. Here *Cassiopea* seems to thrive, and large numbers of them are to be seen lying upon the bottom with their mouth-arms turned upwards, resembling bunches of dark-colored moss.

RATE OF REGENERATION FROM THE PERIPHERY OF THE DISKS WHEN CUT AT VARIOUS DISTANCES FROM THE MARGIN.

It is well to consider first the less complex cases in which an attempt was made to determine the difference in regeneration rates from cut surfaces on the disk of *Cassiopea* at various distances from the margin. Medium-sized medusæ were selected for the experiments, and the cut consisted in each case of the removal of a peripheral strip from the entire disk. Such an

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operation leaves the jelly-fish without marginal sense-organs and, therefore, its rhythmical contractions cease until a slight epithelial rim has regenerated, which serves to reëstablish the pulsation. This new tissue is itself unable to contract, yet it is the seat of the stimulus which causes the disk to pulsate.

Two jelly-fish, each about 86 mm. in diameter, were cut around their entire periphery so as to remove a strip of tissue 10 mm. across (fig. 1). Two other medusæ were cut, in a similar manner as near as possible, and in addition their mouth-arms were removed, so that they were entirely de-

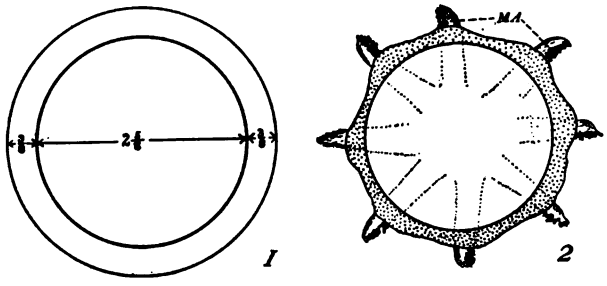

FIG. 1.—Diagram indicating method of cutting.
FIG. 2.—Stippled border shows newly regenerated tissue from cut periphery. New tissue widest where ends of mouth-arms (*MA*) press against it.

prived of all means of obtaining food. The former are designated in table 1 as Nos. 1 and 1A, the latter as Nos. 2 and 2A. By referring to this table the rates of regeneration from the cut peripheries may be readily ascertained for the three medusæ, Nos. 1, 1A, and 2; 2A died soon after the experiment had started. Nos. 1 and 1A were pulsating two days after the operation and in six days they had grown a rim of new tissue 3.3 mm. wide about their cut peripheries. The regenerating tissue then began to thicken and did not increase further in width until after the tenth day. On the fourteenth day the sense-organs were slightly indicated; from this time until the thirty-fifth day there was only a slight increase in the radial width of the regenerating rim until it reached about 5 mm. across, or was one-half as wide as the piece originally removed. During this period, however, the regenerating tissue was becoming thicker, until it had attained the normal thickness of the disk for the given level; further differentiation of the sense-organs was also taking place. At the same time it must be remembered that the animal as a whole was constantly becoming smaller for want of food, so that the disk of No. 1, which measured 66 mm. in diameter after the operation on June 13, measured only 40.6 mm. on July 18, or 35 days later. Thus the amount of regenerated tissue is to the diameter of the disk almost as much as the amount of tissue removed was to the original diameter after the operation was performed.

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TABLE I.—*Regeneration from the cut periphery of the medusa-disk after removal of circular strips of various width.*

Date.	Remarks.	Exp. 1.	Exp. 1a.	Exp. 2.	Exp. 2a.	Exp. 3.	Exp. 3a.	Exp. 4.
June 13	Disk diameter before operation.	86.7	86.7	86.7	64	86.7	86.7	90
June 13	Width of removed margin.....	10	10	10*	10*	16.5	16.5	28
June 19	Width of new tissue.....	3.3	3.3	2.5	Dead.	4	4	4.2
June 21	Width of new tissue.....	3.3	3.3	2.5	.....	5	5	4.2
June 23	Width of new tissue.....	3.3	3.3	3	.....	6.7	6.7	Dead.
June 25	Width of new tissue.....	4.3	4.7	3.3	.....	6.7	5.9	.....
June 27	Width of new tissue.....	4.7	5	5	.....	6.7	5	.....
June 30	Width of new tissue.....	4.7	4.7	5	.....	5	5	.....
July 3	Width of new tissue.....	4.7	4.7	.....	.....	5	4.2	.....
July 6	Disk diameter.....	51.5	45.5	29	.....	29	39	.....
July 6	Width of new tissue.....	5	4.5	4.7	.....	4.6	4.2	.....
July 9	Width of new tissue.....	5	4.5	5	.....	4.4	3.3	.....
July 12	Width of new tissue.....	5	5	Dead.	.....	4.7	3.3	.....
July 18	Disk diameter.....	40.6	33.3	.....	.....	(†)	31.5	.....
July 18	Width of new tissue.....	5.1	4.7	.....	.....	5	3.3	.....

Date.	Remarks.	Exp. 4a.	Exp. 5.	Exp. 5a.	Exp 5b
June 13	Disk diameter before operation.	93.3	96.6	77	
June 13	Width of removed margin.	Disk center only remained.	All of disk removed.	Small strip of disk tissue left.	Same as 5a.
June 19	Width of new tissue.....	6.7	None.....	None.....	None.
June 21	Width of new tissue.....	6.7	None.....	Regenerating from disk tissue.	Regenerating from disk tissue.
June 23	Width of new tissue.....	6.7	None.....	Same as on 21st.	Same.
June 25	Width of new tissue.....	5.3	None.....	Film of tissue over entire top.	Almost same as 5a.
June 27	Width of new tissue.....	(thick) 4	None.....	Same as on 25th.	Same.
June 30	Width of new tissue.....	3	None.....	As on 25th.	As on 25th.
July 3	Width of new tissue.....	3	None.....	As on 25th.	Dead.
July 6	Disk diameter	21	.....	.....	.....
July 6	Width of new tissue.....	4	None.....	Thin film over top (aboral) surface of mouth-arms, regenerated from small pieces of disk tissue.	
July 9	Width of new tissue.....	3.3	None.....		
July 12	Width of new tissue.....	4.6	Dead.....		
July 18	Disk diameter	20	.....		
July 18	Width of new tissue.....	6.5	.....		

* Mouth-arms also removed. † Arched aborally, not measured.

It was observed that those portions of the regenerating rim which were touched or pressed against by the mouth-arms of the medusæ regenerated faster or grew out wider in a radial direction than the intermediate portions which were not so pressed by the arms (fig. 2). This condition may possibly be due to the mechanical pressure of the mouth-arms against such places causing them to thin or flatten out, thus giving a more rapid radial growth, whereas the entire mass of tissue may be no greater here than from other parts of the regenerating surface. I made no observations, however, at the time of the experiments to ascertain whether the new tissue was thin-

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ner at these places where the mouth-arms pressed. Regeneration also proceeded at a faster rate in the irregularities of the cut surface. This case will be fully considered in a following section.

No. 2, which was cut in the same way as Nos. 1 and 1A and in addition had all of its mouth-arms removed, regenerated somewhat more slowly at first, although obviously the most injured of the three. Later, however, it showed almost as much regenerated tissue as either of the other two. During the observations this medusa showed a very peculiar condition; the periphery of the disk became arched aborally and the regenerating tissue was thus also directed aborally, being finally so folded over that the animal became cup-shaped (fig. 3). The regenerating tissue then grew toward the center, and by fusing the edges of its periphery changed the cup into a hollow sphere. This condition was also observed in several other experiments and may be explained thus: The muscles being slightly out of the nor-

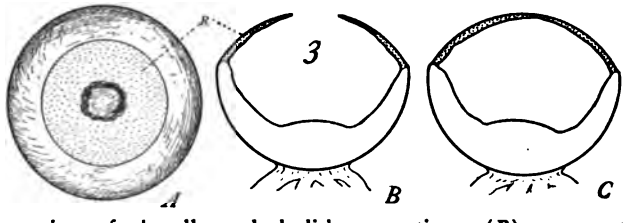

FIG. 3.—*A*, top view of aborally arched disk; new tissue (*R*) regenerating from cut periphery grows toward center. *B*, cross-section of such specimen. *C*, new tissue completely fused over top, converting former disk into hollow sphere.

mal condition of coördination, those expanding the disk act more strongly than the oral contractors and the periphery is thus gradually directed more and more aborally. The new regenerating tissue has a tendency to fuse if two of its surfaces are brought together so that when its periphery is folded aborally and the edges come together they fuse and form the hollow sphere. A similar balloon-like condition has been recorded by Hargitt (1899) in *Gonionemus*. Hargitt was unable to produce such a condition artificially, although he tried in several ways to do so.

Two other medusæ, designated in the table as Nos. 3 and 3A, had a strip 16.5 mm. wide taken from the peripheries of their disks. These disks are, therefore, more injured than the first and they are also cut at a deeper level. After 6 days they had regenerated a rim of tissue slightly wider than that of Nos. 1 and 1A, and after 10 days the rims of the latter were only half as wide as those of Nos. 3 and 3A. From this time the periphery of No. 3 became abnormally arched and its regeneration was slightly modified, yet it continued ahead of Nos. 1 and 1A. The disk of 3A remained flat and the regenerated border here increased rapidly in width for 12 days and then commenced to thicken and ceased to grow in width; the sense-organs began

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to appear after 23 days. The disk had resumed its rythmical pulsation in 2 days after the operation. It will be found by a study of the table that after about 12 days the regenerated tissue began to decrease in width. This fact may be explained by the thickening which the new tissue commences to undergo at this time, or again it may result from the causes which tend to make the entire disk gradually decrease in diameter, until after 35 days it is little more than half as large as it was when the experiment began.

Nos. 4 and 4A were cut so that only the center of the disk covering the bases of the mouth-arms remained. From No. 4 a strip almost one-third as wide as the entire diameter of the medusa was cut away. This disk was 90 mm. in diameter before the operation and only 34 mm. after the removal of the strip. It must also be kept in mind that the cut surface at this level is very thick, since the disk is thickest at the center and becomes thinner as the margin is approached. No. 4 died soon after the experiment started, as is indicated in the table. No. 4A was healthy and within 6 days had regenerated a rim of tissue from its cut surface which was almost twice as wide as that observed in any of the above experiments. After 12 days, here again, the regenerated strip ceased to increase in width, but continued to become thicker. Finally, as is shown in table 1, the rim of new tissue actually began to decrease in width as it had in 3A.

The deep-cut surfaces when regenerating first grow a wide, thin rim of tissue which finally begins to thicken at the expense of radial growth till the normal thickness of the disk at the given level is reëstablished. It will be seen that regenerating tissue from a cut surface near the disk margin widens slowly, but almost continuously, as at this level the disk substance is very thin and no subsequent thickening of the regenerated tissue is necessary.

Three medusæ were now cut so that in two individuals only a small bit of disk remained attached to the mouth-arms and in the third the entire disk was removed. The object of such operations was to ascertain whether the mouth-arms were able to regenerate a disk, or disk-tissue. It was found that the very small portions of the disks which remained would regenerate new tissue, but the mouth-arms were incapable of regenerating from their bases, although they healed the wounded surfaces and lived for 29 days after the entire disk had been removed.

Other experiments on removing strips of various widths from the periphery were made and results closely similar to those above were obtained. One must then conclude that the disk of *Cassiopea* begins to regenerate its margin at a faster rate the nearer the cut is to the center of the disk. A small individual regenerates proportionately faster than a large one. These results are closely similar to those obtained by Morgan on the salamander, fish, and earthworm, and by comparison show that the rates of regeneration differ at different levels of the body, and further that (as in embryonic growth) the nearer the normal body-size or form is approached the slower

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will be the rate of the regenerating growth. Miss King (1898) finds in *Asterias* that the rate of regeneration is greatest from the disk and decreases directly towards the tip of an arm. It is also true that those medusa-disks cut nearer the center are the greatest injured and according to Zeleny would be expected to regenerate their removed tissue fastest, just as they really do. It so happens that the difference in level and the amount of injury are often closely associated. I shall, however, cite an experiment below which serves to contrast the two and shows the level of the cut to be the more important factor in regulating the rate of regeneration.

RATE OF REGENERATION FROM DIFFERENT PARTS OF VARIOUSLY SHAPED CUT SURFACES.

For the study of problems relating to the rates of growth from surfaces partially cut as compared with those entirely cut, and the rates of growth from different parts of the same cut surface, *Cassiopea* offers exceptional opportunity, since the disk-body itself may be cut in sundry patterns and the regeneration rate observed in the several cases. Morgan (1902 and 1906), from a study of regeneration in the fish's fin, has contributed a number of valuable observations bearing on the question in point. The caudal fins of *Fundulus* and *Carassius* were trimmed in different ways, and it was found that partially cut surfaces regenerated slower than entire surfaces cut at the same level; also that new tissue grew out at a faster rate from certain parts of all cut surfaces than from other parts. Since Morgan's experiments were confined to the manner of regeneration from fins or appendages, I determined to make similar cuts upon the disk or "body" of the medusæ to ascertain whether the same principles in regeneration would hold. The results show not only that the same manner of regeneration is adhered to in the body and in the appendages of the two animals, but further, that the forces controlling or determining the regeneration rate on various parts of the cut surfaces act similarly in animals as different as fish and medusæ, almost at the opposite ends of the animal series.

Straight cuts were made upon the disks of medusæ in the following ways: First, a single piece was cut from the disk, as shown in figure 4. Second, two such pieces were cut off as indicated in figure 5, and lastly three pieces were removed as in figure 6. Five individuals were cut in each way and different-sized pieces were removed. The course of regeneration followed by each of the cuts in all of the 15 medusæ was practically the same. The history of one set, consisting of one of each kind of individual, will answer for all.

The specimen having one cut will be designated as A, the two cuts as B, and the three cuts as C. From A a portion of the disk was removed that measured 32 mm. wide at its broadest place and included 6 of the 16 marginal sense-organs. Four days later the regenerated tissue from the cut

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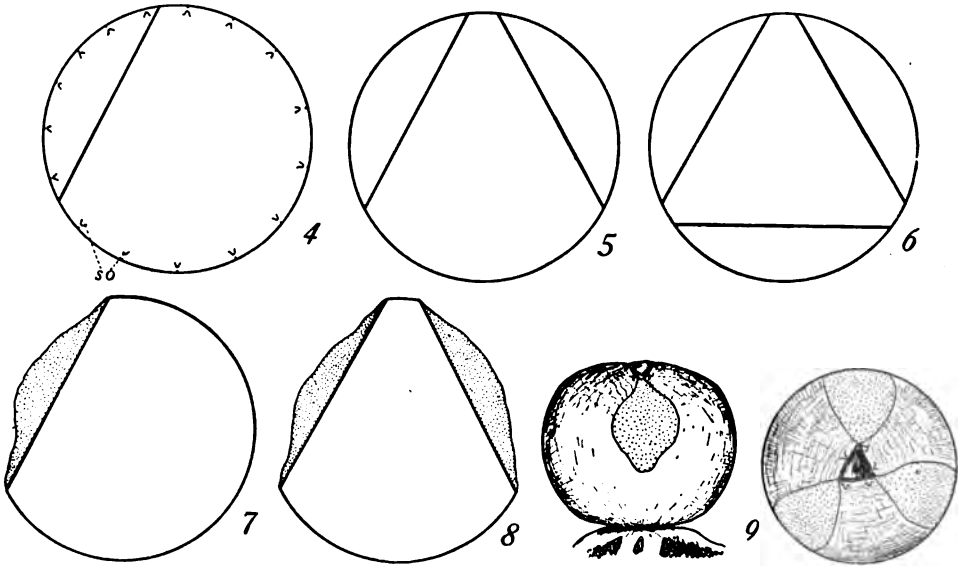
was shaped as indicated in figure 7. The middle part of the cut, which is the deepest part and nearest the disk center, regenerates faster than the sides. After a number of days the middle part goes a little slower and when the cut is 20 days old the regenerated tissues from different parts of the cut surface are about the same widths, although the middle portion is the thicker.

Sense-organs commence to form from the new tissue at this time. The new tissue, being weaker than the other parts of the disk, is sometimes pulled aborally and somewhat folded or puckered, so that it is difficult to measure accurately, though during the first 25 days of the experiment the regeneration rate at different portions of the cut may be accurately measured.

The manner of regeneration from the two cut surfaces of B is identical with that from the single cut of A. In both, then, the rate of regeneration



FIGS. 4, 5, 6—Diagrams indicating ways in which disks were cut to give one, two, and three straight cut surfaces. *SO*, sense-organs.
FIGS. 7, 8.—New tissue (stippled).
FIG. 9.—Top and side views of disk cut as shown in fig. 6. During regeneration the intact corners became aborally arched, modifying the manner of growth and producing hollow spheres with opening at top.

is retarded at the marginal corners of the cut, so that the mid-portion grows ahead of the lateral parts (see fig. 8).

The three cut surfaces of C (fig. 6) follow the same course of regeneration as do those of A and B. Disks cut in this way, however, seem especially inclined to turn their three intact corners aborally, and in so doing the cut surfaces, instead of remaining straight form angles. It will be shown more in detail later that regeneration proceeds much more rapidly in an angular cut than from a straight surface, since the two sides of the

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angle seem to reënforce one another in regeneration, a kind of summation of regeneration occurring. Through such a process the disk is converted into a ball-shaped body with a small triangular opening at the top, where the three uninjured corners are brought almost together (fig. 9).

It will be recalled that the fins of the gold-fish and *Fundulus,* when cut straight across, begin to regenerate their new tissues faster in the middle of the cut and slower near the corners, a fashion identical with that followed by the disk of the jelly-fish.

The medusæ-disks were next cut in such patterns as to give what Morgan has termed "partial cut surfaces" (figs. 10, 11, and 12). Such cuts were varied in the width of their different parts as well as in depth. Many individuals were prepared in the several ways.

The deep part of the cut shown in figure 10 must be wide, since it shows a strong tendency to close its walls together after a week or two (fig. 14). The history of the regeneration from such a cut surface may be recorded in detail. The cut was made so that the bottom of the deep part was 23 mm. from the peripheral margin at its most distant point; this part was 26 mm. in width; the lateral shallow parts of the cut were each 19 mm. wide and 10 mm. below the margin at their middle point. Four days after the operation the regeneration was perceptibly greater from the deep-cut surface than from the lateral shallow surfaces, and within six days the middle part had almost overtaken the lateral surfaces (fig. 13). The regeneration in the deep cut really takes place from three surfaces, the bottom and the two sides of the cut, as here there is free opportunity for lateral regeneration, thus differing from the case of the fish's fin, where the fin-rays seem to prevent lateral regeneration, since they are only capable of growing out from the stumps of the old rays.

Ten days after the operation there was 13 mm. of regenerated tissue from the deep cut and only 10 mm. from the lateral shallow parts. After 14 days the deep cut had become so pulled together that there was only 5 mm. between its original walls. When 20 days old the regenerated tissue had rounded across its free margin and was now growing out as one piece. After 23 days the old sides of the deep cut were only 3.3 mm. apart; the regenerated tissue over it measured only 10 mm. and over the shallow parts 7 mm. This loss in width may be either due to the thickening of the new tissue which is taking place, or may be on account of the general decrease in size which the medusa has undergone, measuring now 63 mm. in diameter, whereas it was 77 mm. across when the experiment began. The new tissue from the deep cut after the twenty-third day began again to increase slowly in width until when 35 days old it was 14.5 mm. wide and that from the shallow parts was 8 mm. The original walls of the deep cut were almost drawn together, being only 2.3 mm. apart. The entire cut had tended to contract, so as to take an angular form, as illustrated in figure 14. All

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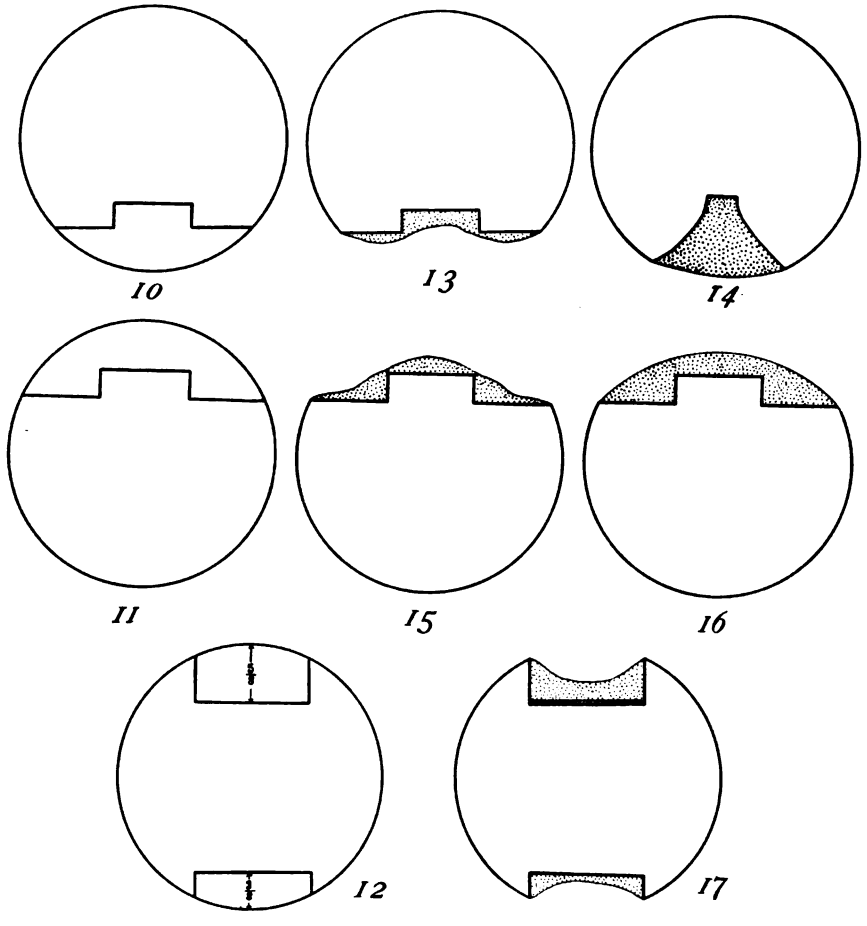
medusæ operated on in this fashion regenerated similarly to this one. Their manner of regeneration may then be briefly summarized as follows:

The rate of proliferation of new tissue is faster from the deep partial-cut surface and slower from the lateral surfaces. The angles of the deep partial cut assist in the regeneration process and thereby help to make it proceed faster from this portion of the cut, whereas the corners of the lateral cuts seem to exert a retarding influence over the rate of regeneration



FIGS. 10, 11, 12.—Diagrams showing manner of cutting medusæ disk to test regeneration rates from partial cut surfaces.

FIGS. 13, 14.—Stippled areas indicate course of regeneration from cut surface of pattern, fig. 10.

FIGS. 15, 16.—Course of regeneration from such a cut as shown in fig. 11.

FIG. 17.—Showing manner of regeneration from fig. 12.

(see fig. 13). Such a conclusion is identical with that reached by Morgan in his study of the regeneration from similar cut surfaces on the fish's fin.

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We may now consider regeneration from surfaces cut in practically the opposite manner from those just recorded. The lateral cuts are deep, with a high middle tongue-piece (fig. 11). Many medusæ cut in this fashion regenerated tissue in a similar way. The exact history of one of the individuals is as follows: The disk was cut so that the lateral surfaces were 26 and 41 mm. wide, respectively, and the high tongue-piece between them was 14.5 mm. wide and 10 mm. high, or above the level of the side cuts (fig. 11). Six days after the operation the newly proliferated tissue was widest on the two side portions and narrow from the middle piece. The corners of the high middle part seemed to exert a retarding influence on the regenerative processes, as did also the outer or marginal corner of the lateral cuts. The inner corners of the side cuts were, on the other hand, the places of greatest regeneration, as no doubt the lateral and basal surfaces both contributed to the process (fig. 15). Nine days after the operation the regenerated tissue from the lateral cuts was 5 mm. wide, while that from the middle piece was only half as much. On the twelfth day the conditions were about the same. The fifteenth day gave the side parts 7 mm. of new tissue, while the middle part had proliferated tissue only 2.3 mm. wide. At this time the old border of the middle piece is 8 mm. wide, while the lateral parts are 16 and 5 mm. respectively. When 21 days old the regenerated tissue had rounded its border (fig. 16) and measured 7 mm. deep over the side cuts and 3.5 mm. over the middle part. From this time until the twenty-seventh day the middle part continued to grow out new tissue, while the side portions seemed to have completed themselves.

Regeneration from such a cut surface may be thus summarized. The lateral cut surfaces produce new tissue faster than the high middle piece. The outer corners of all the cut surfaces seem to exert a retarding influence on the rate of regeneration, while from the inner corners of the lateral cuts new tissue is formed at a very rapid rate, which is probably due to a summation of regeneration. It will be again recalled that an identical condition exists in the regeneration from similar cuts on the fish's tail.

Medusæ were also cut in such a way as to test the rate of growth at different levels on one and the same individual. Here, obviously, the conditions of nutrition and vigor must be as nearly identical as possible. At one place on the rim of the disk a piece was cut out which was 10 mm. deep at its broadest part. Opposite this cut, or 180° away, a second piece of the disk, including an arc of the same extent, was cut away to a depth of 16 mm. from the highest point of the arc (fig. 12). When one cut is narrower peripherally than the other, the rates of regeneration are not readily compared, since regeneration proceeds more rapidly from a narrow cut than from a wide one at the same level.

After six days the regenerating tissue was broader from the deep than from the shallow cut, although here it has a thicker base of tissue to grow

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from; this is also true for the fish's fin, where the deeper cut has a thicker base. Two measurements of the regenerating tissue were made, since the thick base was not exactly a perpendicular surface. The one was from the edge of the old tissue on the aboral surface to the edge of the new tissue, which measured 5 mm. over the deep-cut surface; the other measurement was from the oral border of the old tissue to the margin of the regenerated tissue, 3.5 mm. wide. The rate of regeneration was fastest at the corners in these cuts, being 7 mm. wide at this place in the deep cut. The shallow cut showed 1.5 mm. of new tissue from its middle and 5 mm. from its corners (fig. 17). After 9 days the deep cut had regenerated tissue 7 mm. wide from its middle, while the shallow cut showed only 3.5 mm. of tissue. Both of the cuts were at this time 13 mm. in width peripherally. When 18 days old the cuts were 10 mm. across between the vertical edges of the old tissue, the deep cut had regenerated new tissue 7 mm. wide and the shallow 3.5 mm., or half as much. Here again regeneration proceeds in one and the same individual at a faster rate from the cut surface at the level nearer the disk-center than from a similar more distal cut.

I may now cite an experiment which was made to test whether medusæ would regenerate their sense-organs faster when consecutive ones were removed or when alternate ones were cut away. The experiment threw no light on this question, but the result was curious and for this reason may be mentioned. Two healthy medusæ, one with 16 and the other with 17 marginal sense-organs, were treated as follows: Four adjacent sense-organs were removed from one part of the disk and three alternate ones from the region opposite these. After 23 days no definite trace of regenerating sense-organs could be detected, so all of the remaining old sense-organs were cut away to ascertain whether the new ones were sufficiently regenerated to maintain the pulsation of the disks. The disks became perfectly still after the last one of the original sense-organs was cut off, and only after a period of 6 days was one individual slowly pulsating. This is peculiar, as when the entire peripheral border with all sense-organs is removed the newly regenerated tissue causes the disk to pulsate usually after two or three days. Further, a number of medusæ with regenerated margins had produced sense-organs from their new tissue, while the two above had not regenerated them from their old bases.

REGENERATION AFTER THE REMOVAL OF PIECES OF ORAL EPITHELIUM OF DIFFERENT SIZES AND AT DIFFERENT DISTANCES FROM THE DISK-CENTER — THE QUESTION OF "REGENERATIVE PRESSURE."

These experiments were carried out with the hope of testing whether or not "regenerative pressure," in the sense Morgan (1906) used the term, actually exists and exerts itself from the center radially to the periphery. In other words, is this force felt more towards the center and gradually

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less, as the limits or periphery of the body is reached? This pressure is responsible for the "gradual slowing of regeneration as the normal form is approached, and it is apparent that this retardation will be the same, whether it occurs near the end of an old part or as a new part approaches completion." If this be true it ought also to follow that the pressure conditions of regenerative forces are greater in the center than at the periphery of the disk in *Cassiopea.*

In the experiments, only the oral epithelium and thin superficial muscle-layers were removed. It may be that such experiments are not conclusive, since this pressure might exert itself outward from the face or cross-cut area only, and not so clearly on the surface. At any rate, as will be seen, the results do not lend particular strength to the idea of greater regenerative pressure near the center.

Six medusæ were operated upon as follows: From the oral surfaces of two individuals, Nos. 1 and 1A, two rectangular pieces of epithelium and underlying muscle were removed. The removed tissues had the same width in a radial direction and were equidistant from the periphery, while one piece was longer than the other in the direction parallel to the circumference of the disk (fig. 18). If the pressure exerts itself only in a radial direction, then the two cuts should regenerate at the same rate independent of their peripheral lengths, since they are equally wide. Two other medusæ, Nos. 2 and 2A, had two equal-sized pieces removed from their oral surfaces, one piece being nearer the center than the other (fig. 19). The last two, Nos. 3 and 3A, had one piece running in a radial direction cut from each, as seen in figure 20.

Mayer (1906) has shown that when the epithelium is scraped away on the oral surface of *Cassiopea* an electrical stimulus applied on one side of the abrasion is unable to pass over and stimulate the tissue on the other side. As soon, however, as a very delicate layer of tissue is regenerated over the cut place the stimulus will be transmitted across. This affords a delicate means of detecting the first trace of regeneration.

Twenty-four hours after the above operations No. 3 was scratched on its oral surface so as to divide it into a series of concentric rings (fig. 21). The rings were then scratched across at a place opposite the removed radial strip. The rings of tissue were thus broken at one place, so that no impulse could pass from one of their halves to the other unless tissue had regenerated over the radial injury sufficiently to conduct the stimulus. It would be expected that the inner ring should be the first to conduct. None of the injuries had regenerated sufficiently after 24 hours.

Two days after the operation Nos. 1 and 1A did not transmit across their injuries. No. 2 transmitted the stimulus across the inner area only, although this was equal in extent to the more peripheral injury. The clear, transparent regenerating epithelium could now be seen, and it was noticed

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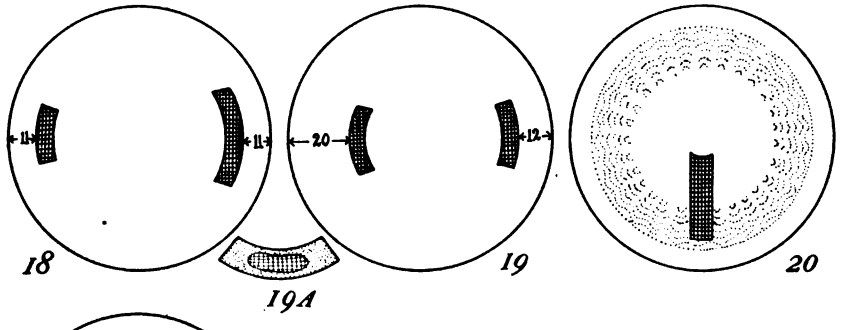
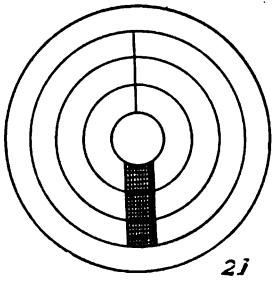
that the growth was greatest at the two ends instead of in the radial direction (fig. 19A). This is probably due to the corners being nearer together at these ends, and regeneration takes place from both sides of the angles, such a summation causing it to proceed faster.

Four days after the operation all of the scars had regenerated tissue sufficiently to cover them completely over. The smaller places had regenerated sooner than the larger ones, yet a comparison of rates of regeneration is difficult to make, since the wounds tend to draw their walls together and





FIGS. 18, 19, 20.—Positions and patterns of pieces of oral epithelium cut away to test force of regenerative pressure from disk-center radially outward. Fig. 19*A*, New tissue growing over rectangular wounds.

FIG. 21.—Manner of scratching circles through oral epithelium to test rate of regeneration from different parts of superficial radial wound.

thus close at the same time that the regeneration is in progress. On the whole this experiment is unsatisfactory.

A somewhat similar experiment was arranged to test the rates of regeneration of epithelial coverings over wounds of different sizes and others of the same size at different distances from the disk center. The sizes of the holes were regulated by means of a sharp cork-borer, which could be used to cut out small circles of exact diameters. Nos. 1 and 1A each had three circular wounds 10 mm. in diameter at 10, 16, and 20 mm. from the margin. Nos. 2 and 2A had three circles scraped, each about 24 mm. from the disk margin and over radii leading to the sense-organs. The circles were 7, 8.5, and 10 mm. in diameter. On 3 and 3A four circles each, 8.5 mm. in diameter, were scraped, 20 mm. from the margin, two of the wounds being over radii leading to sense-organs and two midway between such radii. All four are, however, immediately below radiating canals, so that the difference in regeneration rate, should any be observed, might be attributable to their different nervous connections (fig. 23).

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Two days after the operation Nos. 1 and 1A showed their outermost circles with regenerated films about half over them; the inner circles were in the same condition, but the two circles occupying intermediate distances from the margins had regenerated films of epithelium which entirely covered the wounds. In No. 2, where the three circles were equidistant from the margin but of different diameters, the largest and smallest circles were still not completely covered over, while the one of intermediate size was entirely covered. In 2A all of the circles had regenerated coverings entirely over them. Nos. 3 and 3A showed all of the holes to be 5 mm. in diameter; thus they had become contracted to little more than half of their original size. Those on the sense-organ radii seem a little further covered than those on intermediate radii, though there is very little difference at all.

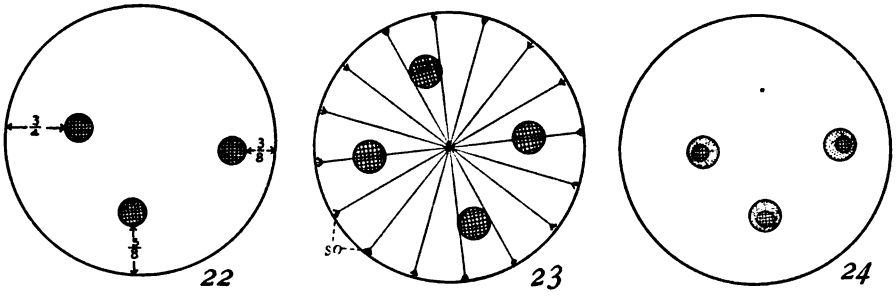

FIG. 22.—Medusa disk with 3 equal sized circular wounds at different distances from margin.
FIG. 23.—Disk with 2 circular wounds over radii leading to sense-organs, and 2 exactly similar wounds between sense-organ radii. *SO*, sense-organs.
FIG. 24.—Regeneration from 3 circular oral wounds.

With these circular cuts one eliminates the angular regeneration factor mentioned in the experiments above, and it was noted in all cases that the film was widest from that area of the circumference toward the disk center (fig. 24). This condition would be expected on the hypothesis of greater regenerative pressure near the disk center, though the deeper level of the cut at this part is a better explanation.

Three days after the operation all of the circles were entirely covered over. These experiments are also difficult to draw conclusions from, since the wounds have a tendency to contract while they are healing and regenerating new tissue. Those nearest the disk center contract most. Thus one might believe them to be more rapidly producing the new tissue.

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THE RATE OF REGENERATION FROM DIFFERENT AREAS ON TAPERING PERIPHERAL STRIPS AND REMAINING PART OF DISK — CONTRASTING THE LEVEL OF THE CUT AND EXTENT OF INJURY.

The circular medusa disk offers exceptional material for certain operations that could not be carried out on animals having a differently shaped body. It has been found difficult to perform an experiment which would clearly contrast the rate of regeneration from certain levels with the rate from parts more or less injured. According to Zeleny the rate of regeneration will be faster the greater the injury up to a reasonable limit, and according to Morgan's pressure and growth idea the rate varies at different levels, being slower as the level is nearer the normal body limits. The conditions are usually open to either interpretation, since the least injured animals are the ones with less body tissue removed and necessarily nearer the normal body limits than those with more tissue removed.

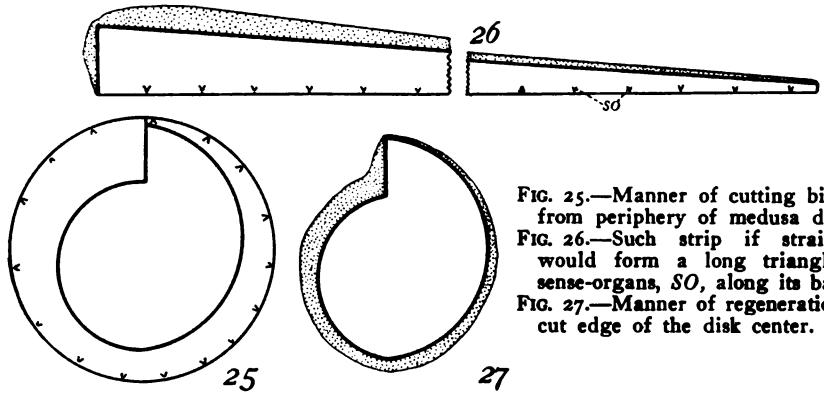

FIG. 25.—Manner of cutting bias strip from periphery of medusa disk.
FIG. 26.—Such strip if straightened would form a long triangle with sense-organs, *SO*, along its base.
FIG. 27.—Manner of regeneration from cut edge of the disk center.

If a medusa disk is so cut that a strip wide at one end and narrow at the other is removed from the entire periphery, then regeneration will take place from the entire cut surface of the strip and also from the cut margin of the remaining disk center (fig. 25). *The strip* is most injured, one may say, at its narrow end, as obviously here more of the disk has been removed from it, and it is least injured at its broad end, as here less tissue has been cut away. The wide end of the strip, however, has more raw tissue exposed by the cut, as the disk is thicker near the center and gradually thinner toward the periphery. One might claim that those portions with the most raw tissue exposed were the most injured; therefore the strip and disk center were equally injured along corresponding regions of the cut. It seems more logical, however, to consider the object most injured from which a greater amount of its original body tissue has been separated. The remaining *disk center* is most injured where it was deepest cut or on that part from which the wide end of the strip came, and it is least injured where the narrower part of the strip came from.

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The rate of regeneration from the strip, which when straightened forms a long triangle, is fastest at the wide end and is gradually slower as the narrow end is reached (fig. 26). In other words, *it is fastest from the part of least injury*. The regeneration rate from the disk part is most rapid in the deep cut and slower as the cut approaches the margin (fig. 27). Here, then, it is *fastest at the place of greatest injury*. In both cases, however, regeneration is fastest at the deepest, or same, level, and slower as the level nears the margin. It is of interest to note that the *regeneration in both directions, toward the periphery and toward the center, proceeds at almost the same rate from the same level.*

It might be claimed that the narrow end of the strip did not have sufficient material for more rapid regeneration, but this is scarcely possible, since the entire strip is in a healthy, vigorous condition and the narrow end might easily draw on other portions for food material. The rate of regeneration at the narrow end is due to its level, and is usually the same as that from the corresponding place on the center disk, or even in some cases the rate of regeneration from the narrow end may exceed that from the same cut area of the disk.

After removal from the disk the strip continues to pulsate, thus having a twisting serpentine motion which often causes it to twist or become folded. Bends and folds form angular-like places along the cut surface and, as mentioned in previous sections of this paper, the shape of the cut exerts an influence on the rate of regeneration. This source of error has been kept in mind and the regenerating tissue from the strips carefully measured on all parts. It was evident that regeneration proceeded in exactly the manner cited above and was oftentimes twice as much from the wide as from the narrow end of the strip within 5 days after the operation.

This experiment seems to contrast in a way the influence due to the degree of injury and those exerted by the different levels of the animal's body upon the rate of regenerative growth. If this be true the level at which the cut is made is the more important factor of the two, and if the extent of injury exerts any influence upon the rate of regeneration it is a secondary influence and probably due only to the fact that the amount of injury and level are closely associated. The greater the injury to a medusa the closer the level is to the disk center.

That such an experiment on the medusa-disk is to be freely compared with experiments in which different numbers of appendages are removed will probably not be generally admitted. I should not like to be understood as claiming that the narrow end of the "strip" bears a similar relation to the wide end as that which the animal with many appendages removed does to the one with few.

This experiment serves further to indicate that activity and rest are negative factors in determining the rate of regeneration. The bias-cut strip is in periodic pulsation from the time it is removed from the central

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portion of the disk, while the latter does not pulsate until a sufficient rim of new tissue has formed around its cut edge, usually requiring about two days after the operation. Yet the rate of regeneration is practically the same from corresponding parts of the two pieces. The physical condition of the strip and center piece must be closely similar, since they are parts of the same individual. It is important to remember here that the sense-organs and a part of the nerve-ring accompany the strip, while the central part has much less nervous tissue; yet this fact seems to cause no difference in the rate of regeneration of new tissue from the two pieces. The question of the influence of activity and rest will be attacked in a more conclusive manner in the next section.

REGENERATION DURING ACTIVITY AND REST—WITH AND WITHOUT RHYTHMICAL CONTRACTIONS.

Zeleny has suggested, with reservation, that when several appendages are removed, the effort to use the regenerating ones, or exercise, may cause the buds to grow faster. The general question of the influence of the nervous system on regeneration is an important one. Since *Cassiopea* is an animal with a rhythmically pulsating movement, it seemed likely that an experiment might be so arranged as to test the influences of activity and rest on the rate of regeneration. With such an idea in view a number of experiments were performed, the most satisfactory being recorded below.

A ring about 20 mm. in width was cut from the margin of the disk. The sense-organs were removed from half the periphery of this ring, while equal-sized pieces of tissue between the sense-organs were cut from the other half, the degree of injury thus being practically equal on the two halves. If, then, the epithelium was scraped across between the sense-organ half and the other without sense-organs, the first half continued to pulsate, while the latter comes to rest (see fig. 28, A). Such a ring will regenerate tissue toward the center until the circular space is covered over. Careful measurements were made on six preparations of this kind with two controls which had the entire ring in motion and two others with all the ring at rest. Comparing all measurements, it seems as though the tissue was regenerated at approximately equal rates from the two halves (fig. 28, B). From this experiment one is unable to find any reason to believe that activity or effort is capable of accelerating the regeneration rate. In this animal the rate of regeneration seems to be independent of the nervous impulse necessary for activity. The experiments given in the previous section, as well as those to be considered in connection with the influences of various salt solutions on the rate of regeneration, also furnish some evidence on the question of activity and rest as determining factors.

Child (1904) has, in a number of contributions upon the subject of Regulation, held that activity exerts a marked influence upon the manner of regeneration. He has also claimed that the nervous system exerts an in-

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direct influence over the regeneration rate through its control of the animal's movements. The experiments recorded above, however, seem to contrast (in a manner only possible on some such unique form) the effects

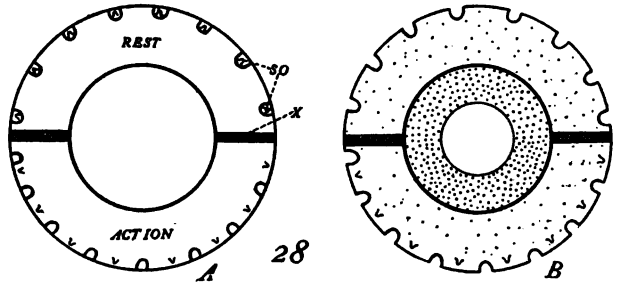

FIG. 28.—Ring from which disk center has been cut away. *A: so*, sense-organs cut away from upper half; from lower half equal-sized pieces have been removed. *X*, insulation between halves. *B:* Stippled area shows rate of regeneration to be equal from the two.

of activity and rest, and the results show in a decided way the negative influence of the two conditions. If such facts apply to the animal kingdom generally, then Child's idea that the regulation of growth is controlled by these factors is insufficient to account for the observed phenomena.

THE RELATIONSHIP BETWEEN THE NUMBER OF REMOVED MOUTH-ARMS AND THEIR RATES OF REGENERATION.—DOES THE REGENERATION RATE OF AN APPENDAGE VARY DIRECTLY WITH THE EXTENT OF INJURY?

The conclusion that the animal with the greater number of removed parts regenerates each part more rapidly than does the one with the lesser number of removed parts was suggested by Zeleny (1903, 1905) and supported by his studies on several forms. He (1903) found in *Ophioglypha,* the brittle-star, that when three or four of the arms were removed from an individual each arm would regenerate faster than would the arms of an individual with a smaller number removed. The difference in rate was sufficient to be shown in his text-figures (1905, fig. 4). The arms of this star-fish are all similar in size and form, and thus the regenerating bud from the base of any one may be compared with that from the base of any other. Such an animal also regenerates the arm-buds by a process of continuous growth. No criticism that I know of can be cited against these observations on *Ophioglypha* nor against Zeleny's conclusion that in this species at least the rate of regeneration is fastest in the series which has undergone the greatest injury, except possibly the objection that the series consisted of too few individuals. It may be that while in one group of animals results similar to Zeleny's would obtain, in another different results might follow. This can only be ascertained by further observations.

It will be shown below, from a study of several series of *Cassiopea,*

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in which all of the mouth-arms are, likewise, almost similar in size and form and regenerate by a process of continuous growth, that wide variations are presented in the rate of regeneration of the several arms. The series with a few removed arms may regenerate each arm as rapidly as do those with a greater number of removed arms. An individual with several arms cut away often shows as great variation in the regenerating rates of the different arms as is found on comparing the average rates of individuals with few and many arms removed. Here it may be emphasized that the variation in regeneration rates of the several arms of one and the same individual (a variation shown to exist only slightly in most of Zeleny's tables, but which is very striking in some of mine) is an index to the dangers which arise when one compares the average rates of regeneration found in several different individuals. Miss King (1898) also states in her study of regeneration in *Asterias* that "the rate of growth of the new arms is ordinarily unequal when a disk regenerates two or more at the same time."

Zeleny has studied three forms of decapod Crustacea—*Gelasimus, Alpheus,* and *Cambarus,* the crayfish. He realized that so few individuals of *Gelasimus* and *Alpheus* were available for final comparison that it was unsafe to draw general conclusions. In these two forms the chelæ are of unequal size and in *Alpheus* they undergo a reversal upon removal of the larger one. (See Prizibram, 1901, and Wilson, 1903.) Zeleny cites such facts as introducing complications in this study. The crayfish, *Cambarus,* has the two chelæ of equal size and for other reasons also is better suited to regeneration experiments. After a careful study of 77 individuals, 61 of which were available for the final comparison, Zeleny concludes:

> That in the series with the greater degree of injury each chela regenerates more rapidly than the single removed chela of the series with the lesser degree of injury. Likewise [and this is the point that I shall attempt to show the importance of in interpreting Zeleny's experiments] the members of the series with the greater injury molt more rapidly than those of the series with the lesser injury.

This work on the Crustacea seems to me to be open to criticism. Such animals must molt before the regenerating bud is observed. The time elapsing between the operation and the first molt varied from 27 to 181 days, and according to Zeleny, "the amount of regeneration of the right chela at the end of the first molt is the same, no matter what the degree of injury may be." Further, "The specific amount of regeneration at the end of the first molt after the operation is a constant which is not affected by the time of the molt, the size of the animal, or the degree of other injuries to the individual." It seems almost inconceivable that one animal should thus require nearly seven times as long to regenerate a bud of a given length as was necessary for another to grow a similar bud.

Zeleny now takes this "constant" (specific amount of regeneration at the end of the first molt) and divides it by the number of days between

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the time of operation and the first molt and considers the quotient as the "specific rate of regeneration per unit of thoracic length per day." As quoted above, "the members of the series with the greater injury molt more rapidly than those of the series with the lesser injury." Thus it clearly follows that any "constant" divided by fewer days (a smaller number) will give a greater quotient (specific rate of regeneration per day) than the same "constant" divided by a greater number of days. The calculations included in Zeleny's tables 6 and 7 (1905) then, to my mind, fail to show that the greater degree of injury causes a faster regeneration, but merely that those most injured molt sooner after the operation; and since all regenerate the same specific amount at the end of the first molt regardless of the time, of course the ones molting soonest will appear to grow that specific amount quickest.

A more plausible line of reasoning would seem to be the following: Since all have the same specific amount of regeneration after the first molt, whether it takes 27 or 181 days for the molt to occur, this specific amount probably begins to be formed soon after the operation and continues until it is prevented by the chitinous covering of the crayfish, just as the animal's increase in body-size is always checked by the amount of expansion possible within its inflexible case. When the growth is so checked it must stop and remain quiescent until the molt occurs. The full amount of growth may be attained in 10, 20, or 30 days—no one can say—but after it is once attained all succeeding days until the molt occurs are not days of growth at all, but merely a quiescent period. That some such process as this is followed is strongly suggested by the fact that the specific amount of regeneration is a "constant" for all at the time of the first molt.

It is not at all certain, then, that the regeneration is continuous throughout the period elapsing between molts; therefore, one is in error to divide the specific amount of regeneration, a "constant," by the number of days between molts and to consider the quotient obtained as the specific rate of regeneration per day. The columns of specific rates in Zeleny's tables 6 and 7 mean nothing, unless it can be proven that the regeneration is continuous during all of the 27 or 181 days, and since the columns of specific amounts show this element to be practically constant it seems likely that all of the individuals regenerate as much as possible soon after the operation and then the process stops until the molt occurs.

To further illustrate the insufficiency of such a method of calculation we may consider the line of averages at the foot of Zeleny's table 6. The specific amount of regeneration for series A averages 0.444 and for series B (the ones with greater injury) 0.435 (practically equal), while the average specific rate of regeneration for A is 0.0049, and for B almost twice as much, 0.008. The columns including the number of days before the molts are not averaged, but if one will make the calculation for the 14

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cases in series A, he will find the average period before molting to be 97.43 days, while for the 13 individuals of series B it is only 60.77 days. If now the average molting period of series A be multiplied by its specific rate of regeneration, we have $97.43 \times 0.0049 = 0.4774$, and a similar calculation for series B gives $60.77 \times 0.008 = 0.4861$. The two products differ but slightly. Thus the average specific rates of regeneration for the two series are to one another as the average times between the operation and the first molts. The average line of Zeleny's table 7 gives a similar result ($0.42 = 0.633$), but not so close as the above, where the two series have almost the same number of individuals, 13 and 14; in Zeleny's table 7 series A contains 14 and B 20 individuals. The only legitimate conclusion to be drawn from such figures seems to be that *Cambarus* regenerates a given amount (the specific amount of regeneration) and stops until a molt occurs; if the molt comes early, then the animal has an opportunity to continue its regeneration; and so it may be said that a crayfish which molts oftener will regenerate a limb sooner than one molting less often. Thus if greater injury causes the crayfish to molt more promptly, they grow a limb sooner merely on account of having more opportunity to grow, as the result of frequent molts, but whether the specific rate of regeneration is more in those with the greater degree of injury is not definitely shown.

Zeleny states: "The more rapid regeneration of the limbs may be the cause of the acceleration of the molting, or the opposite may be the case, or finally the two phenomena may be coördinate and only indirectly related." In the crayfish it seems that the greater injury is accompanied by more rapid molts, but I see no proof that the latter response results from a more rapid regeneration. It may be due to the regeneration taking place from a greater area.[1]

Of special interest in this connection are the results of Emmel (1907) on the lobster. Only an abstract of Dr. Emmel's paper has yet been published. He has written me, however, that the specific amount of regeneration at the time of the first molt was fairly constant, and this is the important point for comparison with Zeleny's results. Emmel found that those individuals with the greater degree of injury molted slower, while those less injured molted faster. The response is opposite to that of the crayfish. The significant point is his conclusion that the rate of regeneration was slower in the more injured series and faster in those less injured—again an opposite conclusion from that of Zeleny.

If Emmel's observations that the lobsters most injured molt slower than those less injured is correct, then his second conclusion of slower regeneration from those most injured is clear. In the lobster, as in the crayfish, the regenerating bud grows as long as possible and then is pre-

[1] Emmel (1906) has shown that it is the process of regeneration itself which affects the rate of molting in the lobster.

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vented from going further by the hard chitinous shell; this amount of growth (specific amount of regeneration) may very probably be attained some time before the ecdysis. Now, if we follow Zeleny's method of first calculating the specific amount of regeneration and then dividing this by the number of days elapsing between the operation and the molt, we get a slow rate of regeneration for those most injured, since they molt slower and give a larger number of days as a divisor with the specific amount of regeneration as a constant dividend. With such a method of calculation it is not a question of regeneration rate at all, but merely a consideration of the molting period. Emmel states that the later the mutilation is made in the molting cycle the more rapid is the rate of ensuing regeneration. This suggests that the regenerating bud may grow to its limit within the encasing wall in a very short time, and when the molt is long postponed it must remain quiescent for a long period.

I have entered into this somewhat detailed criticism of the work on crustacea, since it seems to me that in considering the rate of regeneration one finds himself on rather uncertain grounds when using an animal on which the continuous growth of the regenerating part can not be observed. On the other hand, *Cassiopea* is well suited to such study, since all of its eight mouth-arms are similar and the regenerating buds from the stumps of the arms grow continuously and may be constantly observed and measured.

Sixteen healthy individuals were selected and their disks carefully measured. They were arranged in eight series of two individuals each, having one mouth-arm removed from each of the first pair, two arms from the second, and so on to the seventh pair, where seven mouth-arms were removed from each. The eighth pair had four alternate arms removed. After 4 days none showed any marked indications of regenerating buds. Two weeks after the operation distinct buds were regenerating from the cut arm-stumps, though at this time it was almost impossible to determine whether there was any difference in rate. Later, however, differences in rate became evident.

By referring to table 2 comparisons may be readily made between the average specific amounts of regeneration from those medusæ with a few mouth-arms removed and those with many. The first column indicates the number of arms removed from the individual; the next column gives the diameter of each disk at the time of the operation; the third column gives the specific amounts of regeneration for the medusæ 20 days after the operation. This specific amount of regeneration is the quotient obtained when the average length of the regenerating buds from the stumps of the several arms is divided by the aboral diameter of the medusa disk. The fourth, sixth, and eighth columns show the diameters of the medusæ at intervals during the experiment. It will be noted that the animals were

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gradually decreasing in size, probably due to an insufficient food supply. It should be recalled, however, that Morgan has shown for a number of forms that starvation or lack of food does not affect the rate of differentiation in the regenerating processes. Further, all animals in my experiments were under identical conditions, so that they are to be compared without regard to food supply. The fifth, seventh, and ninth columns give the specific amounts of regeneration at the times indicated. In these tables it is unnecessary to calculate a specific rate of regeneration per day, since the growth was continuous and each column of specific amounts is given for a certain number of days; obviously the specific amounts divided by the same number of days are to one another as their quotients would be. Thus the first column of specific amounts not only indicates the specific amounts of regeneration for each individual up to that time, but also the relative rates of growth during the 20 days.

At 20 days after the operation one individual with only one mouth-arm removed and both medusæ with two arms removed have regenerated faster than any of those with four or five removed arms. The ones having lost six and seven arms show faster regeneration than any others of the series. These four medusæ are, however, the smallest individuals, and young small medusæ usually regenerate faster than larger ones, even under the same conditions. The medusæ with four alternate arms removed are going at about the same rate as the two above with four adjacently cut arms. All medusæ in the table, with the exception of the last two, had consecutive or adjacent arms removed.

After 23 days the medusæ have decreased somewhat in size, as is shown by comparing the second and fourth columns. At this time, July 6, the fifth column, specific amount, shows a sudden jump when compared with the third column. This is not an actual jump occurring within the three days' time between the calculations, but is only apparent, since the specific amounts after 20 days were calculated on the basis of the original diameters of the medusæ and the calculations at 23 days are made on the diameters at this time.[1] The two columns are not to be compared. The other columns to the right are open to comparison, since the diameters were remeasured each time. The specific rates of regeneration for the individuals with one, two, and three arms removed are about the same. Those with four removed arms have a slight advantage over those having lost five arms; it must be mentioned, however, that one individual with five arms removed has failed to produce a bud from one stump and consequently its average regeneration is abnormally low. Again the ones with seven cut arms are regenerating fastest of all, and those that lost six follow next.

On the 18th of July, 35 days after the operation, the regenerating buds

[1] Recent studies show that only the original diameters are to be used in such calculations, as final diameters vary with different extents of injury.

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were all growing at a healthy rate, as is readily seen by comparing the specific amounts of regeneration with those of July 6. Individuals with two, three, four, and five arms cut away are going at similar rates, although showing irregular fluctuations. A point of some importance is that there is a greater difference in regeneration rates between the two individuals with three arms cut away than between any others of the series having lost from two to five mouth-arms. Those with six and seven removed arms still lead in the rate of regeneration. The two with four alternate arms cut away are going at about the same rate as the two with four consecutive mouth-arms removed.

The experiment was closed after 38 days, at which time the longest buds were slightly less than 9 mm. in length. These were produced by the medusæ in which four and five arms had been removed, which were among the largest individuals of the series. Those with one and two cut arms were regenerating at about equal rates. The two individuals with three removed arms showed a great difference between their average regeneration rates. Those with four arms removed were regenerating faster than those that had five arms cut away. Those with six and seven cut arms led the series, but, as mentioned above, these were the smallest individuals. The two with four alternate arms removed were perceptibly behind those with the four adjacent ones cut away.

TABLE 2.—*Average specific amounts of regeneration from medusæ with their mouth-arms removed.*

June 13.		July 3.	July 6.		July 18.		July 21.	
No. of arms removed.	Diameter.	Specific amt. of regeneration.	Diameter.	Specific amt. of regeneration.	Diameter.	Specific amt. of regeneration.	Diameter.	Specific amt. of regeneration.
1	3.5	0.0289	3.37	0.0492	2.87	0.0869	2.75	0.0909
1	3.5	.0357	2.75	.0454	2.37	.0526	2.25	.06
2	3.25	.0387	2.75	.0567	2.25	.0833	2.19	.0857
2	3.25	.0387	2.75	.0426	2.25	.0694	2.19	.0714
3	3.37	.037	2.56	.0469	2.25	.1111	2.06	.126
3	3.37	.037	2.75	.0418	2.5	.05	2.37	.0526
4	3.62	.0344	3.12	.0685	2.5	.079	2.62	.1025
4	3.62	.0344	2.75	.056	2.37	.1084	2.37	.132
5	4.12	.029	3.5	.0608	2.87	.0956	3	.1
5	4.12	.029	3.5	†.0351	2.69	†.0604	2.87	†.0652
6	2.5	.052	2.19	.0765	1.75	.0997	1.87	.1116
6	2.5	.05	1.93	.0893	1.62	.1346	1.69	.1659
7	2.25	.0833	1.43	.1304	1.16	.1643	1.19	.1583
7	2	.0937	1.60	.0953	1.25	.1500	1.31	.1664
*4	3.5	.0328	3.5	†.0357	3	†.0416	2.93	†.0372
*4	3.5	.0388	3.5	.0625	3	.0833	3	.0885

* Four alternate mouth-arms were removed, in all others adjacent arms were cut away.
† No regeneration at all from one arm-stump.

Table 2, as a whole, indicates a condition of individual variation and fluctuation in the regeneration rates rather than anything else. It should

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be mentioned that these calculations have been made, according to the usual custom, from linear measurements only, but it must be borne in mind that the actual volume of new tissue might oftentimes be more in a short stocky bud than in a longer slender one. Some of the regenerating arm-buds are short and branching, while others are long and simple in structure.

There is no doubt that the individuals with six and seven removed arms, those of the greatest degree of injury, regenerated at a faster average rate than the other medusæ of the series. It should be remembered that these were the smallest, and, as a matter of fact, in all of the experiments the small young medusæ showed more ability to regenerate rapidly than did larger old ones. Unfortunately this point was not controlled, although indirectly it is checked by a comparison with the other members of the series which are practically of a common size. In the last column, for instance, those medusæ with three and four removed arms are regenerating at a better rate than those having lost five arms, and they are also slightly smaller than the latter, although they were all of practically the same size.

The objection to this experiment, which has probably suggested itself before this time, is that too few individuals were employed. This objection is not as serious as it may seem at first sight. If among animals any such general law of regeneration exists as that the greater the degree of injury the faster the rate of regeneration, it should at least manifest itself to an evident degree. It is not necessary to use more than half as many medusæ to satisfy one's self that the rate of degeneration is fastest from the middle of a straight-cut surface and slowest from its outer corners; that regeneration is faster from a level 20 mm. from the disk margin than from any level less than that distance from the margin; that regeneration takes place fastest from the widest end of a peripheral bias-cut strip of the medusa disk and slowest from the narrow end of the strip; or, that a number of other conditions will follow, depending upon the manner in which the disk is cut. These are all facts in regeneration, and a number of them are shown by distantly related animals; and, if the degree of injury determines the rate of regeneration to any significant extent, it seems to the writer that it should manifest this determination in a more evident manner.

A serious objection to the view of a connection between the degree of injury and the rate of regeneration is the fact that from a single medusa the several arm-buds grow out at rates differing as widely as the average rates of individuals with different degrees of injury. It is difficult to understand how such a fact can be reconciled to the degree of injury idea. When one individual has six arms cut away, each at the same distance from its base, then it would be expected that all of the arms should regenerate at almost the same rate, for there is little doubt that the degree of injury is the same in each case and the surrounding conditions are as near as possible identical, being similar places on the body of one individual.

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TABLE 3.—*Specific rates of regeneration from each stump of two removed arms on the same individual.*

Individual.	July 6, 23 days.			July 18.			July 21, 38 days.		
	Diameter.	Length of arm-buds.	Specific amt. of regeneration.	Diameter.	Length of arm-buds.	Specific amt. of regeneration.	Diameter.	Length of arm-buds.	Specific amt. of regeneration.
A.....	2.75	0.125	0.0454	2.25	0.125	0.0555	2.187	0.125	0.0571
	2.75	.187	.0681	2.25	.25	.1109	2.187	.25	.1142
B.....	2.75	.115	.0418	2.25	.125	.0555	2.187	.125	.0571
	2.75	.12	.0436	2.25	.187	.0833	2.187	.187	.0857

Table 3 gives the histories of each arm in two individuals which had had two of their mouth-arms cut away. The individual A shows after 23 days a greater variation between the rates of regeneration from its two arm-stumps than is shown in table 2 between the average rates of all the medusæ with one, two, three, five, and four (alternate) arms removed. At the thirty-fifth and thirty-eighth days one of the arms has grown twice as fast as the other. The B individual of table 3 also shows a distinct difference in regeneration rates between the two arms.

TABLE 4.—*Specific rate of regeneration from each stump of four removed arms on the same individual.*

Individual.	July 6, 23 days.			July 18.			July 21, 38 days.		
	Diameter.	Length of arm-buds.	Specific amt. of regeneration.	Diameter.	Length of arm-buds.	Specific amt. of regeneration.	Diameter.	Length of arm-buds.	Specific amt. of regeneration.
A.....	3.125	0.187	0.06	2.5	0.156	0.0625	2.62	0.187	0.0714
	3.125	.188	.0603	2.5	.187	.075	2.62	.264	.1006
	3.125	.23	.0736	2.5	.196	.0785	2.62	.312	.119
	3.125	.25	.08	2.5	.25	.1	2.62	.312	.119
B.....	2.75	.126	.0458	2.37	.224	.0945	2.37	.305	.1284
	2.75	.136	.0496	2.37	.241	.1013	2.37	.308	.1297
	2.75	.166	.0604	2.37	.252	.1062	2.37	.311	.1311
	2.75	.187	.0681	2.37	.312	.1315	2.37	.33	.1389

Table 4 gives the histories of each of four arms in two individuals, A and B. Here again one finds as much variation in the regeneration rates as is shown between the average rates for individuals with different degrees of injury in table 2.

Table 5 records the rates for each of the six regenerating arms in two individuals, A and B. The individual A shows a variation in rate of regeneration between the first two arms in the table and the last one which is greater than the difference in average rates of regeneration between almost any of those variously injured medusæ given in table 2. The individual B of table 5 also shows a variation in the rates of regeneration from its several arm-stumps.

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TABLE 5.—*Specific rate of regeneration from each stump of six removed arms on the same individual.*

Individual.	July 6, 23 days.			July 18.			July 21, 38 days.		
	Diameter.	Length of arm-buds.	Specific amt. of regeneration.	Diameter.	Length of arm-buds.	Specific amt. of regeneration.	Diameter.	Length of arm-buds.	Specific amt. of regeneration.
A.....	2.187	0.1249	0.0571	1.75	0.125	0.0714	1.87	0.125	0.0666
	2.187	.1297	.0593	1.75	.139	.0792	1.87	.135	.0718
	2.187	.1875	.0857	1.75	.153	.0873	1.87	.187	.1
	2.187	.1875	.0857	1.75	.187	.1071	1.87	.253	.1343
	2.187	.1875	.0857	1.75	.193	.1103	1.87	.262	.1397
	2.187	.1875	.0857	1.75	.25	.1428	1.87	.313	.1671
B.....	1.94	.122	.0627	1.63	.125	.0769	1.69	.189	.1121
	1.94	.167	.0862	1.63	.187	.1153	1.69	.25	.1481
	1.94	.187	.0967	1.63	.25	.1537	1.69	.303	.1794
	1.94	.187	.0967	1.63	.25	.1537	1.69	.31	.1836
	1.94	.187	.0967	1.63	.25	.1537	1.69	.312	.1851
	1.94	.187	.0967	1.63	.25	.1537	1.69	.315	.1869

With such remarkable variations existing within the same individual in the regeneration rates of its arms, it is dangerous to draw conclusions from the differences shown in rate of regeneration among the individuals of a small series. As pointed out above, the variations in rate between pairs of similarly injured individuals in table 2 are as great as the differences in rate between two individuals which have suffered different degrees of injury. It must be recognized, finally, that in these medusæ the individual variation in regeneration rates is sufficient to conceal a minor variation which might be due to the degree of injury, did such exist.

These tables giving the specific amount of regeneration from the arm-bases of the same individual serve, at least, to indicate that no deductions can be made from table 2 regarding the specific amounts of regeneration from medusæ injured to greater or less degrees. Tables 3, 4, and 5 indicate still further that unless the differences in regeneration rates among animals injured to greater and less degrees are constant and marked they may very likely be accidental, or else due to the peculiar responses of that given form upon which the experiment was conducted. It is of interest to note that Scott's (1907) study of regeneration in the fish's fin and the present data from the medusæ both indicate that the extent of injury is negative in its influence on the rate of regeneration. Zeleny and Emmel's results on animals that must molt in order that the regenerating bud may continue to grow are due, I believe, to the influence of the regenerating tissue on the molting cycle.

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THE INFLUENCES OF CHANGED CHEMICAL CONDITIONS ON THE RATE OF REGENERATION.

At present scarcely anything has been ascertained as to the effects produced upon regenerating tissues by changes in their chemical environments. Loeb (1904) found that *Tubularia* in a solution slightly below the concentration of sea-water would regenerate more rapidly than in normal sea-water. It was also necessary to have the solution slightly alkaline, in order to obtain a maximum growth. Loeb also made some observations on the influence of the oxygen supply and found, as in the case of embryonic growth, that an insufficient amount of oxygen retarded the rate of regeneration. A series of experiments that I (1906, 1907*a*, 1907*b*) have conducted on the developing fish egg has shown that although in a new medium the embryo may often develop to all appearances in a normal manner, yet its rate of growth is usually affected.

In the following experiments the four elements Na, K, Ca, and Mg were employed, as they seem so essential to marine life, and also form a group, as it were, the members of which act against one another or fit together in ways so as to produce a favorable balance for the maintenance of life-processes.

Mayer has performed a number of most instructive experiments illustrating the influences of these elements upon the rhythmical pulsations of *Cassiopea*. He found that sodium stimulates slightly the muscular activity and that it is "the chief stimulant of sea-water." A combination of Na, K, and Ca is, however, a greater stimulant. Magnesium must be present in order to hold such a combination in check and thus sustain a rhythmical action. Normal medusæ are but little affected by an excess of NaCl in sea-water and will pulsate for more than 18 hours in sea-water plus 1 per cent excess NaCl. A 1.55 per cent excess of NaCl was found to give rapid pulsations and to shrivel the medusa disk. A relative excess of K and Ca retards pulsation, even though the actual amount of K and Ca is that contained in sea-water.[1]

Potassium temporarily stimulates and then retards pulsation; in excess it is quite poisonous. The disk comes to rest expanded, with the mouth-arms contracted. In a 0.125 per cent excess of K_2SO_4 the rate of pulsation is reduced to half the normal after 13 hours, while 1.55 per cent excess will stop the pulsations within 4 minutes.

Calcium itself is not necessary for pulsation, although by its presence the inhibiting effect of Mg is counteracted. After one has inhibited pulsation in a given manner it may be restored in solutions lacking Ca, showing that this element is unessential for rhythmical contraction. A 1 per cent sea-water solution of $CaCl_2$ reduces the rate of pulsation; recovery is immediate in sea-water.

[1] By sea-water Mayer means Van't Hoff's artificial sea-water and the retardation which he attributes to Ca and K in this sentence may in reality be due to the smaller relative amount of Na present in the solution.

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Magnesium salts in sea-water retard pulsation and reduce its rate, amplitude, and energy. The disk will pulsate at twice its normal rate in sea-water minus magnesium. In a 1.6 per cent sea-water solution of $MgCl_2$ the disk pulsates slowly for half an hour and then stops.

The medusæ in the following regeneration experiments were subjected to the influences of sea-water concentrated to two-thirds and three-fourths of its original volume; or to sea-water diluted with distilled water, two parts of sea-water to one of distilled and one of sea-water to one of distilled; or to sea-water solutions of $NaCl\ \frac{m}{12}, \frac{m}{15}, \frac{m}{30}$, and $\frac{m}{50}$; $KCl\ \frac{m}{40}, \frac{m}{50}, \frac{m}{75}$ and $\frac{m}{100}$; $CaCl_2\ \frac{m}{20}, \frac{m}{50}$, and $\frac{m}{100}$ and $MgCl_2\ \frac{m}{20}, \frac{m}{40}$, and $\frac{m}{80}$. The medusæ were all cut as shown in fig. 29. The margin of the removed piece included four of the peripheral sense-organs and was made as near as possible of the same proportional size in the several medusæ.[1]

The regeneration of these medusæ is shown in tables 6 and 7, which have been arranged from two experiments run at different times. In the first column of these tables the solutions employed are listed; the second and fifth columns contain the diameters of the individuals at the times indicated, the third and sixth columns give the exact amounts of regeneration that have taken place in a radial direction from the middle of the cut surfaces; the fourth and seventh columns show the specific amounts of regeneration from the different individuals. These last amounts may be compared also as specific rates of regeneration per day, since all have consumed like periods of time in the regeneration process.

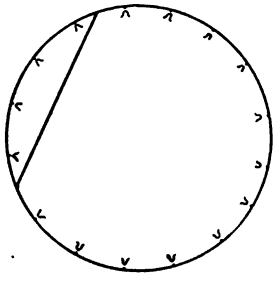

FIG. 29.—Diagram of disk with straight cut removing four of its marginal sense-organs.

The rates of pulsation of the medusæ disks were retarded in all of the solutions after the first several hours, the retardation being more marked in some cases than in others. The pulsations were always, however, slower than the controls.

The animals in the sea-water concentrated to two-thirds its original volume died within two days. Those in the three-fourths concentrated sea-water were so weakened that they showed no beginning of regeneration and were placed in normal sea-water after the third day. The diluted sea-water solutions also had a decidedly depressing effect. All medusæ in such

[1] Those in table 6 treated with $KCl\ \frac{m}{50}$ and $MgCl_2\ \frac{m}{40}$ were small individuals, as indicated, and were cut in the dovetailed way shown in figure 10. This no doubt accounts in part for their apparently rapid regeneration, for it will be recalled that the deeper portion of a cut of this shape regenerates at a faster rate than a straight cut, such as that in figure 29.

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media regenerated at a slow rate and threw out masses of slimy material, a reaction commonly shown when this animal is placed in disagreeable surroundings. It is recognized that the concentration and dilution of these sea-water preparations are very great and with slight concentration or dilution such injurious effects might by no means follow. The one object of the powerful solutions was to ascertain whether this animal was very resistant to changes in the osmotic pressure conditions, and the fact that they existed in these solutions for such long periods of time indicates that they are not particularly sensitive to osmotic changes.

TABLE 6.—*Rates of regeneration in strange chemical environments.*

Solutions.	July 4. Experiment 6 days old.			July 6.		
	Diameter.	Length of new tissue.	Specific amt. of regeneration.	Diameter.	Length of new tissue.	Specific amt. of regeneration.
Control	2.75	0.155	0.0568	2.56	0.25	0.0975
NaCl $\frac{m}{12}$	2.25	.093	*.0416	----	-----	(†)
KCl $\frac{m}{40}$	1.87	.048	.0249	1.75	.063	.0357
KCl $\frac{m}{50}$	0.81	.093	‡.1153	0.75	.063	‡.0833
KCl $\frac{m}{100}$	2.37	.125	.0526	1.31	.129	.099
$CaCl_2$ $\frac{m}{20}$§	1.62	‖ None	------	1.5	.031	**.0208
$CaCl_2$ $\frac{m}{50}$	1.13	None	------	1.06	.063	††.0588
$CaCl_2$ $\frac{m}{100}$	2.62	0.146	0.0595	2.25	.187	.0833
$MgCl_2$ $\frac{m}{20}$	2	.071	.0469	1.87	.125	.0666
$MgCl_2$ $\frac{m}{40}$	1.25	.093	‡.075	1.19	.125	‡.1052
$MgCl_2$ $\frac{m}{80}$	2.75	.093	.034	2.75	.16	.0568

* Back to sea-water.
† Dead.
‡ The cut on this individual is differently shaped, see the text.
§ The $CaCl_2$ caused a slight precipitate to form in the sea-water solutions.
‖ Tetanus, put into sea-water.
** In sea-water.
†† Put into sea-water.

A close study of the tables indicates that NaCl slightly retards the regeneration rate, but the weakened appearance of the disk in the strengths of this medium used suggests that the retardation is not a direct effect of the Na, but more probably due to the animal's loss of tone.

The stronger solutions of KCl also retard regeneration. The weaker solutions, on the other hand, seem to accelerate the process so that the specific amount of regeneration from individuals subjected to their action is slightly greater than that of the control medusæ.

The medusæ in the KCl solutions have their disks fully expanded, but their mouth-arms are contracted and balled up in the center.

The $CaCl_2$ solutions produce a tendency toward tetanic contractions and in the stronger solutions the oral surface of the disk is often torn by this violently contracted condition. Mayer (1906) has called attention to this effect of $CaCl_2$ on *Cassiopea*. The rate of regeneration in all of the $CaCl_2$ solutions was slower than normal.

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In table 7 the weaker $MgCl_2$ solutions seem to have caused the regeneration processes to proceed at a rate well ahead of the control. In table 6, however, the indicated effect is not so favorable.

TABLE 7.—*Rates of regeneration in strange chemical environments.*

Solutions.	July 19. Experiment 9 days old.			July 21, 11 days old.		
	Diameter.	Length of new tissue.	Specific amt. of regeneration.	Diameter.	Length of new tissue.	Specific amt. of regeneration.
Control	2.5	0.187	0.075	2.5	0.188	0.075
Sea-water concen. $\frac{3}{4}$	2.25	.125	*.0555	2.28	.187	†.0821
Sea-water diluted $\frac{1}{8}$	2.44	.093	.0384	2.44	.093	.0384
Sea-water diluted $\frac{1}{2}$	3	.031	‡.0104	3	.062	§.0208
NaCl $\frac{m}{15}$	2.31	.095	.0405	2.44	.125	.0512
NaCl $\frac{m}{80}$	2.13	.125	.0583	2.13	.13	.0583
NaCl $\frac{m}{50}$	2.31	.125	.054	2.25	.16	.0694
KCl $\frac{m}{80}$	2.06	.031	.0151	2	.063	.0312
KCl $\frac{m}{75}$	2.12	.142	.0661	2.25	.16	.0694
KCl $\frac{m}{100}$	1.94	.125	.0645	1.87	.187	.1
$MgCl_2$ $\frac{m}{250}$	1.87	.031	.0166	1.75	---	(**)
$MgCl_2$ $\frac{m}{40}$	1.69	.125	.074	1.69	.187	.111
$MgCl_2$ $\frac{m}{80}$	2.37	.187	.0789	2.31	.25	.1085

* In normal sea-water third day.
† In sea-water and regenerating very rapidly.
‡ Medusa throws out slime.
§ Ceased to secrete the slime.
** Disk inverted and new tissue torn away.

These experiments show, on the whole, no marked indication of differences in the specific actions of the several ions upon the rates of regeneration. The experiments are few, but even so they indicate the very complex nature of growth and regeneration processes which are dependent upon so many secondary influences and interactions that it will be found difficult to determine when an element is producing a direct effect upon the regeneration rate or whether the effect is due in some indirect way to other conditions incited by the actions of the chemical used. At any rate, there is evident need for an extensive and careful study along these lines with the view of analyzing, as far as possible, the relationships between regeneration rate and definite osmotic and chemical changes.

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SUMMARY AND CONCLUSIONS.

I. When a peripheral ring of tissue is removed from the disk of *Cassiopea* the cut margin of the disk promptly begins to regenerate a new rim. The rate at which the new tissue is formed depends upon the width of the removed ring. The wider the ring is radially, or, in other words, the nearer the cut is made to the disk center, the faster will the resulting regeneration take place. Cuts made deep into the body of the disk regenerate tissue which increases rapidly in radial width for about ten or twelve days and then almost ceases to grow in width and begins to thicken until the new tissue is as thick as the medusa disk at the given level. The cut periphery from which only a narrow ring of tissue has been removed regenerates slowly, but almost continuously, as this portion of the disk is thin and only a slight subsequent thickening is necessary.

A small medusa regenerates proportionately faster than a larger one.

These facts are closely similar to those observed by Morgan on the earthworm, fish, and salamander. The result is interesting in that it shows that animals so distinctly different as a medusa and a vertebrate regenerate new tissues at rates which differ with different levels of the body, and that as in the process of embryonic growth the nearer the normal body size and form is approached the slower will be the rate of regeneration.

The disks cut nearest the center are injured to the greatest degree, and they might be expected to regenerate new tissue at a faster rate than those cut further from the center or less injured, if the condition is parallel to the removal of more parts. It so happens, however, that the difference in level and the degree of injury often coincide. These two factors were contrasted in other experiments, which seemed to indicate that the level of the cut was the more important in regulating the regeneration rate of the new tissue.

II. *Cassiopea* regenerates new tissue from the wounded edges of straight cuts, and "partial cut surfaces" in exactly the same manner as Morgan found regeneration to take place from similar cuts made on the fins of fishes. Such a fact is of importance; first, since it shows the same principles in regeneration to apply to the proliferation of new tissue from the appendages and the true body-surface of animals. Second, it indicates that a common principle or law regulating the rates of regeneration from different parts of variously shaped cut surfaces runs through the animal kingdom, since forms at almost opposite ends of the series, the fish and the medusa, regenerate in the same manner.

The outer corners of cut surfaces seem to exert retarding influences upon the rate of regeneration at all levels. At the inner corners of "partial cut surfaces" regeneration proceeds at a faster rate than on the straight surface. This fact is probably due to a summation of regeneration which takes place from the two sides forming the angle of the inner corner. (See figs. 13, 15, and 17.)

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III. Experiments were performed to test the rate of regeneration after removal of different-sized pieces of oral epithelium at the same distance from the center and pieces of the same size at different distances from the disk center. My interpretation of Morgan's idea of "pressure" in regeneration would lead one to expect greater pressure near the center and, therefore, new epithelium should cover the more central wounds of equal size sooner than it does those more peripherally located. The experiments were not entirely satisfactory on account of a tendency of the wounds to contract while healing or regenerating new tissue. Those nearest the disk center seem to contract most, so that the result is difficult to interpret. It was noted, however, that in the circular wounds the regenerating film was widest toward the disk center, as if tissue was being proliferated out from that direction at a faster rate than from any other. (See fig. 24.)

IV. When a medusa disk is cut so that a strip wide at one end and narrow at the other is removed from the entire periphery (fig. 25) regeneration will occur along the cut edge of the strip and also from the cut margin of the remaining disk center (figs. 25, 26, and 27). In such a preparation the strip has had most body-tissue removed from its narrow end; also it is least injured at the broad end, where least tissue has been removed. The disk center is most injured where it was deepest cut or at that place from which the wide end of the strip came and least injured on that portion from which the narrow end was cut.

The rate of generation from the strip, which when straightened would form a long triangular body, is fastest at the wide end and is gradually slower as the narrow end is reached. *It is, therefore, fastest from the part from which the least tissue has been removed.* The rate of regeneration from the disk portion is more rapid from the deep-cut part and becomes slower as the cut approaches the region of the former margin; therefore, *the regeneration rate here is fastest from the portion from which most tissue has been removed.* In both cases it will be observed that it is fastest at the deepest or same level, and slower as the level nears the margin. It is important to note that regeneration in both directions—toward the periphery and toward the disk center—proceeds at almost the same rate from the same level.

This experiment may be interpreted as contrasting the influences due to the degree of injury and those exerted at different levels of the animal's disk-shaped body. The level at which the cut is made is shown to be the more important factor of the two, and if the amount of injury exerts any influence on the rate of regeneration it is probably of secondary importance. One could scarcely claim that the narrow and wide ends of the strip were to be compared with two animals from which many and few appendages had been removed.

V. A ring 18 or 20 mm. in width or wider may be cut from the peri-

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phery of a medusa disk and will regenerate from its cut edge until the central space is grown over with new tissue. Such a ring freshly cut had the sense-organs removed from half of its periphery, while equal-sized pieces of tissue between the sense-organs were removed from the other half, thus making the degree of injury equal on the two halves. The oral epithelium was then lightly scraped across between the sense-organ half and the other without sense-organs. After the last operation the first half continued to pulsate, while the latter came to rest, since the stimulus for pulsation seems to be derived from the sense-organs and can not be transmitted across the scraped epithelium (see fig. 28). This ring regenerates tissue toward the center until the space is covered over. The rate of regeneration from the half at rest and the half in motion is on comparisons with the controls found to be the same. The results with this medusa show that activity or effort is not capable of accelerating the regeneration rate, as authors have held to be the case in other animals. This is the most decisive experiment that I know of as a direct test of the influences of action and rest on the rate of regeneration from tissues under as nearly as possible identical conditions, being similar united portions of one individual.

VI. Medusæ having one or more of their mouth-arms removed regenerate these mouth-arms at irregular rates which are not closely associated with the number of arms cut away, or, in other words, with the degree of injury. Two medusæ, each having three of the eight mouth-arms removed, may show a greater difference between their average specific rates of regeneration than would be found to exist among the average specific rates of regeneration from individuals with one, two, four, or five mouth-arms cut away. (See table 2.) An individual from which several mouth-arms have been removed in as near as possible similar ways will exhibit as great a degree of variation among the specific regeneration rates of its several arms as will be found to exist among the average specific regeneration rates of many individuals, each having had a different number of arms removed. (Compare tables 3, 4, and 5 with table 2).

Cassiopea is well fitted for experiments of this nature, since the regenerating buds of the mouth-arms grow continuously and may be measured and compared at any time during the experiments. It is of advantage also to have the several mouth-arms almost identical in size and form, as a comparison of the regenerative processes from the individual arms of a single medusa is thus facilitated. Most of the experimental investigations pertaining to the question of the relation between the degree of injury and the rate of regeneration have been conducted on crustaceans. These animals must molt before the regenerating bud can be observed, and since the length of the molting period varies so widely among the individuals the true specific rate of regeneration is difficult to estimate. The regenerating bud very probably grows as much as the confining chitinous covering will

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permit, just as the crustacean's body increases in size until its inelastic case will allow it to become no larger, and must then remain quiescent until the molting time arrives, which may be weeks or even months distant. There is also a great individual difference between the crustacean's appendages, which renders difficult a comparison of the regeneration rates from the different limb-stumps of the same specimen. *Cassiopea* is free from such objections, but it shows so much variation in the specific rates of regeneration from different individuals that it would be difficult as well as misleading to claim from the data, now at hand, that any relationship existed between the degree of injury an individual had sustained and its specific rate of regeneration.

VII. *Cassiopea* seems to be resistant to slight changes in osmotic pressure, as is indicated by its condition in concentrated and diluted sea-water.

(*a*) Regeneration from the disk of *Cassiopea* was slightly retarded in sea-water to which NaCl had been added. This retardation may possibly be due to the direct action of the Na ion, although considering the weakened condition of the medusæ in such solutions they might be expected to regenerate slower than the normal.

(*b*) Strong solutions of KCl also retard the rate of regeneration, but weaker solutions seem to accelerate the process.

(*c*) Solutions of $CaCl_2$ in sea-water have a tendency to cause muscular tetanus, the oral surface of the disk often tearing as a result of the violently contracted condition. The rate of regeneration in all $CaCl_2$ solutions was very slow, in some scarcely any regeneration taking place for a number of days.

(*d*) Magnesium chlorid in sea-water solutions exerts a rather indifferent influence over the rate of regeneration.

The chemical experiments show no marked indication of a difference in the specific action of the several ions upon the rate of regeneration. Even though such a specific influence of these ions does exist, it would be difficult to discover, owing to the complex nature of the processes regulating growth and regeneration. There is evident need of extensive and careful study along these lines.

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APPENDIX.

After the present paper had gone to press Dr. Zeleny published the results of a study on the effect of degree of injury, successive injury, and functional activity upon regeneration in the scyphomedusan *Cassiopea xamachana*.[1] In this paper he concludes that "removal of six of the eight oral arms constitutes the most favorable degree of injury for the regeneration of each arm, and that from this optimum there is a decrease in both directions." The data, however, on which this statement depends is not altogether conclusive. One finds on studying his table that the extremes of variation in regenerative rates among similarly injured individuals are in the large majority of cases greater than the differences between the average specific amounts of regeneration for two groups of individuals injured to different degrees. With such a wide range of variability shown among the few individuals one is uncertain as to the real significance of the table. Nevertheless, the data do seem to show a steady advance in specific rates of regeneration up to a maximum where six arms were removed.

In a general way my results on regeneration of the oral arms might also be interpreted, like Zeleny's averages, to show a gradual increase in regenerative rates with an increase in degree of injury. Zeleny seems inclined to emphasize the importance of this apparent increase in regenerative rates, while I believe the great range of variability in the regenerative rates shown by the small number of individuals studied should not be overlooked and that it renders a general conclusion from such observations very uncertain.

Zeleny's study of the effect of the rhythmical pulsation of the medusa disk on the rate of regeneration may be compared with my experiments bearing upon the same subject. Our results agree and both indicate, contrary to the view of some observers, that functional activity is negative in its influence on the rate of regeneration. Zeleny compared the regenerating margins and centers of medusæ disks pulsating rhythmically with those from other medusæ at rest, and found that in four of the six pairs of cases the non-pulsating individuals regenerated faster than the pulsating ones. In the fifth pair the two were equal, and in the sixth the pulsating individual regenerated faster.

The question might arise whether in my own experiments the influence from the pulsating half may not be conveyed to the resting half. Improbable as is such a view in itself, the interpretation is negatived by my con-

[1] Journal of Experimental Zoölogy, v, 2, pp. 265–274. 1907.

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trols, some of which, as in Zeleny's experiments, consisted of an entire pulsating ring and others of the entire ring at rest.

The level at which the margin is removed determines the rate of regeneration from the cut surface, and this possibility is not mentioned in Zeleny's account. It is difficult to remove a marginal strip of exactly the same proportions from several medusæ, even when careful measurements are made. Slight differences in the depths of the cuts would easily account for the results, but since the rates of regeneration from both the center and outer margin are considered by Zeleny this is in a manner checked. In my "ring preparations" described above, the level of the cut is controlled as far as possible, since the disk center also forms the center of the circular mass of tissue that is removed. Thus the cut surface and the disk periphery are concentric circles; therefore, all places on the cut surface are at a common level. My observations are aided by the fact that the pulsations were continuous throughout the experiment, while Zeleny's rhythmical pulsations always stopped before the end of his experiment.

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IV. SOME INTERNAL FACTORS CONCERNED WITH THE REGENERATION OF THE CHELÆ OF THE GULF-WEED CRAB (PORTUNUS SAYI).

BY CHARLES ZELENY,

Associate Professor of Zoology at Indiana University.

2 text figures and 11 "table" figures.

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SOME INTERNAL FACTORS CONCERNED WITH THE REGENERATION OF THE CHELÆ OF THE GULF-WEED CRAB (PORTUNUS SAYI[1]).

By Charles Zeleny.

INTRODUCTION AND GENERAL STATEMENT OF RESULTS.

The primary object of the experiments described in the present paper was twofold: The quantitative determination (1) of the effect of successive removal of an organ upon its power to regenerate and (2) of the character of the changes, if any, produced in the uninjured parts of the animal by such removals. In connection with the first problem it was found necessary to determine as preliminary steps the common relations in the amount of regeneration, the length of the molting period, and the size or age of the animal. Since these are points of independent interest they are treated in separate sections at the beginning of the paper. The second problem was studied by a comparison of the character of the left chela in normal individuals with its character in individuals having a removed and regenerating right chela.

It was found that the length of the molting period is but slightly correlated with the amount of regeneration of the right chela and the size of the animal. Thus if all operations are made on the day after a molt the length of time elapsing before the next molt has very little to do with the amount of regeneration which takes place during the period. Likewise, animals of a size, which in general are probably of the same age, do not have the same length of molting period. On the other hand, there is a very close correlation between the size of the animal and the amount of regeneration taking place during a molting period.

On the basis of these results the molting period is taken as the unit in the determination of the amounts of successive regenerations. It is found in general that in individual crabs the third regeneration of the right chela is greater than the second, and the second is greater than the first. Since the animals are increasing in size and age during the course of the experiment, and since this may be sufficient to explain the increase in amount of regen-

[1] The experiments were performed at the Marine Biological Laboratory of the Carnegie Institution of Washington at Tortugas, Florida. I am indebted to the officers of the Carnegie Institution for the privileges of the laboratory during June and July, 1906. I wish especially to thank the Director, Dr. A. G. Mayer, for valuable suggestions and for many other courtesies without which the experiments could not have been successfully completed. The material obtained at Tortugas was measured and studied and the data were tabulated at the zoological laboratory of Indiana University during the school year 1906–1907. The present paper is listed as No. 87 of the contributions from the Zoological Laboratory of Indiana University.

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eration, it is necessary to correct the results by obtaining the specific amount of regeneration in each case; that is, the amount of regeneration divided by the cephalo-thoracic length. When this is done the result shows that the first two successive regenerations at least are equal and there is no change in the power to regenerate as a result of successive injury.

A comparison of the left chelæ in crabs which had been regenerating a right chela with the left chelæ in uninjured individuals shows that there is no appreciable change in the left chela as a result of the removal and regeneration of the right chela.

METHODS AND DATA.

The data are based on observations made upon 197 individuals of the gulf-weed crab during June and July, 1906. Specimens varying in size from 3 to 15 mm. were collected and placed in individual dishes, each with a floating piece of gulf-weed. Each crab was numbered and careful record was made of its molting times and other points of interest. The water was changed every day and the animals were fed on the small fish (atherina) every other day. Care was taken to keep all the conditions as nearly alike as possible in all the dishes. Regular observations were made every morning and at this time cast skins were removed and preserved and necessary operations were made. It was found that the increase in size of the animals was confined to the first day after a molt and all operations were accordingly made a day after the molt, so that the relation to the molting time might be alike in all. The operation in every case consisted of the removal of the right chela as its breaking joint. This was effected by injuring the nerve of the appendage with a needle or forceps. The removed appendage started to regenerate as a coiled bud inside of a chitinous sac. The first molt succeeding the operation released the new chela from its sac and allowed it to expand to its normal form. The external dimensions remained stationary after the first day following the molt. The regenerated chela was again removed on the day after the molt, and so on, as long as the time permitted. The cast skins of each molt, the removed right chelæ, and the final animals were all preserved and measured. A complete record of the history of the animals during the course of the experiments was thus obtained. This gives two series of data. The first gives the normal condition of the parts and the second the parts after the first, second, and third regenerations of the right chela. The different stages of each individual were measured and these and other data are collected in table 1. Full explanations are given in connection with the table. The length of the cephalo-thorax is the greatest length (*LL*) and the width the greatest width (*WW*) as shown in fig. 1. The chela-length is the length of the next to the last segment or propodite, as shown in fig. 2 (*LL*). It will be noticed in table 1 that in a great many cases the casts were broken. In most of these the crab had started to eat up its cast before the first day was up. The table includes *all* the measurements and other data without elimination, since

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it seems necessary in investigations of the present character to be very careful in discarding "abnormal" cases. All cases needing special mention, including those not valid for the purposes of the present paper, are indicated by asterisks (*) and are referred to in the notes appended to the table.

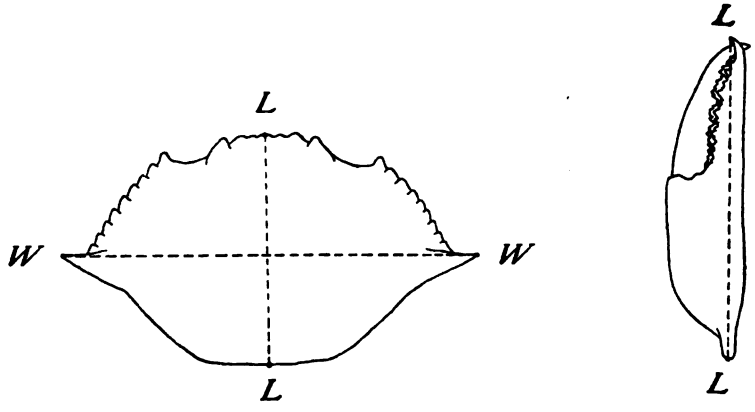

FIG. 1.—Cephalo-thorax of *Portunus sayi*. Dorsal view. × 4. *LL* = greatest length; *WW* = greatest width.
FIG. 2.—Propodite and dactylopodite of left chela (× 5). *Portunus sayi*. *LL* = greatest length of propodite.

To insure further control 24 uninjured individuals were collected at the same time as the others and their measurements are added to the normal series. These individuals are not included in table 1, but are indicated by asterisks in table 15.

RESULTS.

THE COMMON RELATIONSHIP IN SIZE OF THE INDIVIDUAL, LENGTH OF THE MOLTING PERIOD, AND THE AMOUNT OF REGENERATION.

(*a*) *Correlation between the cephalo-thoracic length and the length of the molting period.*—The cephalo-thoracic lengths in millimeters and the lengths in days of the molting periods of all valid individuals are used. For the first regeneration period these data are arranged in order of length of the molting period in table 3 and are shown in coördinate form in table 2. Tables 4 and 5 give the corresponding data for the second regeneration period. For both periods the tables show in a striking manner the low degree of correlation between the cephalo-thoracic length and the length of the molting period.

The conclusion is thus reached that between the limits of 3.9 mm. and 14.5 mm. the length of the molting period is to a large extent independent of the size or age of the animal. This is true when the reservation is made that between the smallest and the largest individuals there is some difference in the average length of the molting period.

(*b*) *Correlation between the length of the molting period and the amount of regeneration of the right chela.*—The lengths of the molting

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periods and the amounts of regeneration of the propodite of the right chela in all valid cases are taken. For the first regeneration period these data are given in order of length of the molting period in table 6 and the same data are plotted in coördinate form in table 7. Tables 8 and 9 give corresponding data for the second regeneration period. An examination of these tables makes it evident that there is but a slight degree of correlation between the length of the molting period and the amount of regeneration. The amount of regeneration which takes place during a molting period is determined only to a very slight extent by the length of that period. It seems, therefore, that the regeneration takes place for the most part during the early days of a molting period and very little increase in size occurs during the later days. For this reason it is not possible in determining the rate of regeneration to use the absolute number of days during which regeneration has taken place.

(*c*) *Correlation between the cephalo-thoracic length and the amount of regeneration of the right chela.*—The cephalo-thoracic lengths and the amounts of regeneration of the propodites of the right chelæ in all valid cases are taken. Table 10 gives these data arranged according to cephalo-thoracic length for both the first and the second regeneration periods. The specific amount of regeneration, that is, the amount divided by the cephalo-thoracic length, is added for each individual. The individuals with a second regeneration are put as nearly as possible opposite individuals of the same size with a first regeneration. For the first regeneration period the data are further shown in coördinate table 11A and for the second regeneration in coördinate table 12. For both periods it is evident that there is a very close correlation between the size or age of the animal and the amount of regeneration of its right chela. With an increase in size there is thus a proportionate increase in the amount of regeneration that takes place during a molting period. This amount of regeneration is independent of the length of the molting period, as has already been shown in the last section. Therefore, in comparing the successive regenerations of the right chela, it is found best to use the molting period as a unit without regard to its length.

A study of tables 10, 11A, and 12 shows a further point of interest regarding the relation between the size of the crab and the amount of regeneration of its right chela. It is seen that as we go from the smaller to the larger individuals the amount of regeneration increases proportionately faster than the size of the animal. In tables 11A and 12 the dotted line is the line of average specific amount of regeneration, that is, the line along which all the measurements would be arranged in case the specific amounts were the same for animals of all sizes. It is seen that for the smaller individuals the measurements of regeneration-length come below the line and for the larger ones above it. Thus the larger individuals show proportionately a greater amount of regeneration than the smaller ones. This result is undoubtedly to be correlated with the fact that there is a corresponding proportionate increase in the size of the chelæ in uninjured individuals.

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This increase is shown for the left chela in table 11C. Here the dotted line is the line along which all the chela measurements would come if all individuals had the same specific length of the left chela. As before, it is seen that the larger individuals have proportionately a larger chela than the smaller ones; that is, the specific length of the chela is greater in the former than in the latter.

COMPARISON OF THE REGENERATIONS OF THE RIGHT CHELA AFTER SUCCESSIVE INJURY.

(*a*) *The successive regenerations in single individuals.*—After the removal of all the possible sources of error that could be found 21 valid cases of successive regeneration remain. Table 13 gives these cases arranged in order of the lengths of the original right chelæ. Table 14 shows the same cases on coördinate paper with the original lengths of the chelæ represented by the abscissæ and the amounts of regeneration by the ordinates. The dotted line is the line of equal length of regenerated and original chelæ. A third regeneration was obtained in only two of the 21 cases. In one of these the first regeneration record is missing. Apart from this the third regeneration is greater than either the first or the second regeneration. In the 20 cases in which the first and second regenerations can be compared the two are alike in 1 individual, the first is greater than the second in 3, and *the second is greater than the first in* 16. Thus, in the great majority of cases, the rate of regeneration increases with the successive removal of the right chela. This result, however, does not take into account the possibility of change in the ability to regenerate due to an increase in size or age. The individual power to regenerate may be changing during the course of the experiment regardless of the removal or non-removal of an appendage. In the following section an attempt is made to eliminate this source of error and to determine whether the successive removal itself has any influence.

(*b*) *A comparison of the first and second regenerations of the right chela in individuals of the same size or age.*—Tables 10, 11A, and 12 have shown that with an increase in size there is a proportionate increase in the amount of regeneration of the right chela. Therefore the difference between the first and second regenerations shown in the last section may be due merely to this factor. A comparison of individuals of similar size is made for the first and second regenerations in tables 10 and 11B. In table 10 individuals of equal size are placed as nearly as possible opposite each other, so that a direct comparison of the amounts of regeneration may be made. In table 11B the abscissæ represent the cephalo-thoracic lengths and the ordinates the chela lengths. The first regenerations are shown by crosses and the second regenerations by circles. The dotted line is the line along which all the marks would be arranged if the specific amounts of regeneration were the same for all sizes of individuals and equal for the first and second

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regenerations. An examination of these tables shows at once that there is no evident difference between the first and second regenerations when the size-difference is eliminated. For equal cephalo-thoracic lengths the amount of the first regeneration is approximately equal to that of the second. The average specific amount for the first regeneration is 0.791 with 66 cases and for the second regeneration 0.789 with 25 cases. The difference between the two is well within the limit of probable error. *Therefore the successive removal of the right chela does not retard nor accelerate the power to regenerate.*

EFFECT OF REMOVAL OF RIGHT CHELA UPON CONDITION OF LEFT CHELA.

Table 15 gives the cephalo-thoracic lengths, the left and right chela-lengths, and the specific lengths of the chela for 165 unoperated individuals.[1] The individuals are arranged in order of cephalo-thoracic length. The specific length of a left chela is the left chela-length divided by the cephalo-thoracic length. Table 11C shows the correlation between the left chela and the cephalo-thoracic length in the same individuals. The dotted line is the line of average specific chela-length; that is, the line along which all the data would be arranged if the specific lengths were alike for all sizes. Tables 16 and 11D give the corresponding data for individuals which have regenerated a right chela for the first time and tables 17 and 18 for second regeneration cases.

Tables 15 and 11C show that in unoperated individuals the left chela length is closely correlated with the cephalo-thoracic length. The average specific length of the left chela is 0.982, but an examination of the tables shows that smaller individuals have comparatively smaller chelæ than the larger ones, a fact which has already been referred to above.

Tables 16 and 11D for first-regeneration cases and tables 17 and 18 for second-regeneration cases show that there is no evident difference between the lengths of the left chela in these individuals and those in unoperated individuals. *The left chela is not influenced by the removal and regeneration of the right chela.* This is readily seen when the coördinate tables are superposed. Furthermore, the average specific length for first-regeneration cases is 0.993 and for second-regeneration cases 1.011 as against 0.982 for the unoperated cases. This progressive increase for the regeneration cases is, however, fully accounted for by the greater average cephalo-thoracic length of the regeneration cases as compared with the unoperated ones and by the fact that the specific amount of chela-length increases with the size of the individual.

[1] *Relative sizes of the right and left chelæ in uninjured individuals.*—In is interesting to note that the right chela is, on the whole, larger than the left. Of the 165 individuals whose chela-lengths are tabulated the two chelæ are of equal size in 49, the left chela is greater than the right in 19, and the right is greater than the left in 97. The average length of the propodite of the left chela is 5.77 mm. and of the right chela 5.84 mm., an advantage of 0.07 mm. in favor of the right chela.

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DISCUSSION.

The relation between the molting period and the size or age of the crab.—Observations on Crustacea show that in general the molting period increases in length with age. In *Portunus sayi* this is true only to a very limited degree in animals between the sizes of 3 and 15 mm. It is probable, however, that very small individuals have a shorter molting period and very large ones a longer one. It is interesting to note in this connection that various observations have been made indicating an irregularity in the molting periods at different ages. Thus, in crayfish, Andrews finds that the increase in length of the molting periods with age is not regular.

The relation between the length of the molting period and the amount of regeneration taking place during the period.—The periodic casting of the exoskeleton in Crustacea and its profound physiological effect upon the whole organization of the animal introduces a factor which has important bearings upon the rate of regeneration. The nature of this relation is imperfectly known, but recent work by Emmel (1906) and others has thrown considerable light on the subject. It is evident that in dealing with Crustacea the molting factor must be eliminated as nearly as possible. One source of error was eliminated in the present experiments by making all operations on the day after a molt, so that all might have the same relation to the molt. The further question arose as to whether or not the length of time between the operation and the molt has any relation to the amount of regeneration. In other words, does regeneration go on at a uniform rate, regardless of the length of the molting period? The results of the present experiments show that, other things being equal, there is very little difference between the amount of regeneration in long periods and in shorter ones. This statement needs only the qualification that between the longest and the shortest periods there is an obvious difference between the amounts in favor of the longest periods, but this is not sufficient to give these a rate of regeneration even approximating to that of the shortest periods. This result makes it necessary in dealing with the comparison of amounts of regeneration to disregard length of time and to use the molting period as a unit. At least this is necessary until the common relations of molting period, size of animal, time of operation with reference to the molt, and amount of regeneration have been more fully worked out than they are at present.

The relation between the cephalo-thoracic length and the amount of regeneration.—Some work has been done upon the effect of age of an individual upon its power to regenerate. The general conclusion has been reached that the power to regenerate is less highly developed in older than in younger individuals, though notable exceptions to this rule have been found. In most of this former work the statements made have been un-

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satisfactory, because of the few cases on which they are based and because of the lack of quantitative data.

In *Portunus sayi* it has been found that the amount of regeneration of the right chela increases regularly with the size of the animal between the limits of 3 and 15 mm. This increase is slightly greater than the increase in size, so that large individuals have a greater specific amount of regeneration than small ones. This increase in specific amount of regeneration is similar to the increase in specific length of the chela with size in unoperated individuals. Thus the chela regenerates at a rate which is proportional to the size of the removed chela, and when the regenerated chela-length is divided by the removed chela-length a quotient is obtained which is fairly constant for all sizes of individuals.

The effect of successive injury upon the regeneration of the right chela.— The effect of successive removal upon regeneration is mentioned again and again in the literature, but almost always in an indefinite way. According to the usual statement, a part capable of regeneration may be removed many times in succession without affecting its power of regeneration. The observed facts upon which this statement is based are as indefinite as the statement itself. The only definite contrary data I have been able to find are referred to in Stewart's Physiology, where the statement is incidentally made in describing an experiment on the regeneration of the sciatic nerve in the dog that the second regeneration was more rapid than the first.

The experiments on the gulf-weed crab (*Portunus sayi*) were made with the object of getting definite quantitative data regarding the relation between successive removal and regeneration. This form was chosen because it is desirable to use an appendage with a definite breaking joint, insuring the absolute indentity of the plane of removal in every case. It is evident that a slight difference in the plane of the cut may have a great influence upon the regeneration. The Crustacea, however, have a very obvious disadvantage. This is the molting habit. The regenerating chela in *Portunus* is coiled up within a chitinous sac until the time of molting. Another disadvantage connected with the same habit is the fact that the comparative character of regeneration at different times during the molting period has not been satisfactorily worked out. As stated above, this disadvantage has been eliminated as far as possible by making all operations at the same time with relation to the molt, namely, on the day after the molt, and by using the molting period and not the day as a unit of regeneration time. The latter was made possible by the determination of the fact that the length of the molting period influences the amount of regeneration only to a very slight degree within the limits of the experiment.

It was found that the amount of regeneration increases with successive removal. An investigation of the relation of this increase to the increase

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in age of the animal, however, shows that it is due not to the successive removal and regeneration, but to other factors connected with the increase in age. In animals of equal size the first and second regenerations are equal, and successive removal neither accelerates nor retards the rate of regeneration.

It is interesting to compare this with former results. As stated above, the general statement has been made again and again that successive removal in many animals does not affect the power of regeneration. In none of the cases upon which this conclusion is based, however, was any correction made for change due to increase in age. If the present experiments had been left on a similar basis the data would have shown an increase in rate of regeneration with successive removal. It is only after the correction for increase in age is made that successive removal is seen to have no influence upon the regeneration of the right chela. The single case of the sciatic nerve of the dog mentioned by Stewart would probably, however, still show an increase in the rate of regeneration after correction for age increase. The general significance of a single case is, however, doubtful, because of the possibility of some physiological change apart from successive injury.

A discussion of the facts of successive regeneration is reserved until the writer has worked up other experiments which are now under way. It is obvious that an exact determination of the effect of successive removal of an organ upon its power to regenerate is of importance in a study of the character of the mechanism at the basis of the process of regeneration.

The effect of removal of the right chela upon the condition of the left chela.—Numerous experiments and general observations point to the conclusion that the removal of one of a pair of organs in cases where regeneration does not take place is followed by an increase in size and efficiency of the remaining organ. Thus, when an arm is removed the other arm increases in size and strength. The same holds for the kidney and other organs. It is of interest to determine whether in case the removed organ starts to regenerate the uninjured organ still undergoes a similar increase in size or efficiency. This matter is of considerable importance in a discussion on the one hand of the factors involved in hypertrophy and on the other hand of the factors concerned in the regeneration of the new organ. If the hypertrophy is due to an excess of production of certain formative or food materials, due to the absence of one of the consuming organs, and a regenerating appendage uses the same material, it is probable that in case regeneration takes place the uninjured organ will not increase in size. This is the result obtained in the case of the chelæ of *Portunus sayi*. The left chela is not larger in animals with a second or a first regeneration of the right chela than in animals of the same size with the right chela uninjured. This result is of special interest, because in *Portunus* the regenerating chela

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does not begin to function as such until after the molt succeeding an operation. The whole chela function during this period is, therefore, carried on by the left chela, which, according to a common theory of hypertrophy, ought to increase in size because of this increase in function. Since it does not, it seems probable, if growth is dependent upon the presence of certain formative or food substances, that the excess of these is directed to the regenerating appendage. The conclusion may thus be reached that the regenerating appendage uses in its growth the same kind of material as that used by a growing uninjured chela. Furthermore, it follows that the distribution of this material is not necessarily determined solely by the exercise of its typical function by the organ in question.

This statement is offered merely as a suggestion, because the data of the present study are not sufficient for a comprehensive discussion. The method with proper control gives promise of considerable value in obtaining an understanding of the internal factors involved in hypertrophy and regeneration.

SUMMARY.

(1) Individuals of *Portunus sayi* with a cephalo-thoracic length between 3.9 and 14.5 mm. show but a slight correlation between the length of the molting period and the size or age of the animal.

(2) The amount of regeneration of the right chela between the same limits of size is likewise but slightly correlated with the length of the molting period, but is very closely correlated with the size of the animal.

(3) The specific amount of regeneration of the right chela increases slightly with increase in size or age of the animal.

(4) The specific length of the left chela in uninjured individuals increases slightly with increase in size or age of the animal.

(5) The proportion between the amount of regeneration of a chela and the length of the chela in uninjured individuals of the same size is a constant uninfluenced by the size of the animal.

(6) In single individuals the third regeneration is greater than the second and the second is greater than the first.

(7) When the correction for change in the power of regeneration with size or age is made it is found that successive removal neither retards nor accelerates the regeneration of the right chela.

(8) The right chela is slightly larger than the left in a great majority of the individuals.

(9) The removal and regeneration of the right chela produces no change in the growth of the uninjured left chela.

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Explanation of Table I.

Original = Original condition of crab as indicated by cast skin of first molt or dead animal in case of death without a molt.
First molt = Condition of crab between first and second molts, as indicated by cast skin of second molt or dead animal in case of death before second molt.
Second molt = Condition of crab between second and third molts.
Third molt = Condition of crab between third and fourth molts.
Date = Date of molt, death, or removal of right chela.
Desc. = Description, as follows: *c* = Cast skin. *d* = Animal died. *k* = Animal killed. *o* = Right chela removed. 1st = first regeneration. 2nd = second regeneration. 3rd = third regeneration.
Cephalo-thorax: *Lg.* = greatest length in mm.; width = greatest width in mm.; *b* = broken.
Left chela = length of propodite in mm. as indicated in fig. 2 (*LL*); *b* = broken.
Right chela: *Lg.* = length of propodite in mm. as indicated in fig. 2 (*LL*); *b* = broken.
An asterisk before the catalogue number indicates that there is a note or notes on that individual. The part of the individual history to which the note belongs is indicated by an additional mark at that part.

Table I.—*Table of data.*

Catalog No.	Sex.	Original.							
		Date.	Desc.	Cephalo-thorax.		Left chela.	Right chela.		
				Lg.	Width.		Date.	Desc.	Lg.
1394	--	June 25	*c*	3.5	6.0	3.3	June 16	*o*	3.3
*1395[1]	--	July 6	*c*	4.4	8.6	4.2	July 6	*c*	*b*
1396	--	July 11	*d*	4.3	7.2	4.0	July 11	*d*	4.0
1397	♂	June 20	*c*	*b*	*b*	*b*	June 20	*c*	*b*
*1398	♂	June 23	*c*	*b*	*b*	*b*	June 16	*o*	3.4
1399	♂	June 29	*c*	*b*	*b*	*b*	June 29	*c*	*b*
*1400	♂	June 17	*c*	*b*	*b*	*b*	June 17	*c*	*b*
*1401	--	June 28	*c*	4.8	8.9	*b*	June 28	*c*	4.9
*1402	--	June 27	*c*	4.8	8.7	4.7	June 16	*o*	4.8
*1403	♂	July 7	*c*	5.8	11.1	26.0	June 16	*o*	[2]4.7
1404	♂	June 22	*c*	*b*	*b*	*b*	June 22	*c*	*b*
1405	♂	July 7	*c*	*b*	*b*	*b*	July 7	*c*	*b*
1406	♂	June 23	*c*	*b*	9.0	*b*	June 23	*c*	*b*
*1407	♂	June 22	*c*	*b*	*b*	[3]*b*	June 22	*c*	[3]*b*
*1408	--	June 19	*c*	*b*	*b*	*b*	June 16	*o*	*b*
*1409[4]	♂	June 19	*c*	*b*	*b*	*b*	June 19	*c*	*b*
1410	♂	June 29	*c*	6.5	12.0	*b*	June 16	*o*	6.5
1411	♂	June 26	*c*	*b*	*b*	6.7	June 26	*c*	6.8
1412	♂	July 2	*c*	7.0	12.2	*b*	July 2	*c*	*b*
1413	♂	June 23	*c*	*b*	*b*	*b*	June 23	*c*	*b*
1414	♂	June 19	*c*	*b*	*b*	*b*	June 19	*c*	*b*
*1415	♂	June 19	*c*	*b*	*b*	*b*	June 16	*o*	*b*
*1416	♂	June 21	*c*	*b*	*b*	*b*	June 21	*c*	*b*
*1417	♂	June 19	*c*	*b*	*b*	*b*	June 19	*c*	*b*
*1418	♂	June 19	*c*	*b*	*b*	*b*	June 16	*o*	7.0
1419	♂	June 20	*c*	*b*	*b*	*b*	June 20	*c*	*b*
*1420	♂	June 20	*c*	8.6	16.2	9.4	June 20	*c*	9.4
1421	♂	July 6	*c*	*b*	*b*	7.4	July 6	*c*	9.0
1422	♂	June 19	*c*	6.0	10.9	6.1	June 19	*c*	6.1
1423	♂	July 5	*c*	8.7	*b*	*b*	July 5	*c*	9.3
1424	♂	July 2	*c*	*b*	*b*	*b*	July 2	*c*	10.1
1425	♂	July 6	*c*	*b*	*b*	12.1	July 6	*c*	*b*

[1] 1395. Died in molting.
[2] 1403. Right chela is smaller than left and is probably a regenerated structure.
[3] 1407. Right chela smaller than left.
[4] 1409. June 25, third left leg missing.

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TABLE I.—*Table of data*—Continued.

Catalog No.	Sex.	Original.							
		Date.	Desc.	Cephalo-thorax.		Left chela.	Right chela.		
				Lg.	Width.		Date.	Desc.	Lg.
*14265	♂	June 22	*c*	*b*	*b*	*b*	June 22	*c*	*b*
1427	♂	July 1	*c*	*b*	*b*	13.2	June 16	*o*	12.9
1428	♂	June 29	*c*	*b*	22.0	*b*	June 22	*c*	14.0
1508	--	June 26	*c*	*b*	*b*	*b*	June 26	*c*	*b*
1509	--	June 25	*c*	*b*	*b*	*b*	June 25	*c*	*b*
1510	--	July 9	*c*	4.2	7.3	3.9	July 9	*c*	3.9
*1511	--	June 26	*c*	3.3	5.8	*b*	June 26	*c*	*b*
1512	♂	July 12	*c*	4.5	7.9	*b*	July 12	*c*	4.3
1513	--	June 21	*c*	*b*	*b*	*b*	June 21	*c*	*b*
1514	--	June 29	*c*	*b*	*b*	*b*	June 29	*c*	*b*
1515	--	June 26	*c*	*b*	*b*	*b*	June 26	*c*	*b*
1516	--	July 1	*c*	*b*	*b*	*b*	July 1	*c*	*b*
*1517	--	June 25	*c*	3.8	6.2	*b*	June 25	*c*	*b*
*1518	♂	June 30	*c*	3.0	5.3	*b*	June 30	*c*	*b*
*1519	--	June 22	*c*	*b*	*b*	*b*	June 22	*c*	*b*
1520	♂	July 6	*c*	*b*	*b*	*b*	July 6	*c*	*b*
*1521	♂	July 7	*c*	*b*	*b*	*b*	July 7	*c*	*b*
*1522	♂	June 30	*c*	*b*	8.1	*b*	June 30	*c*	*b*
1523	♂	June 25	*c*	*b*	7.9	*b*	June 25	*c*	*b*
1524	♂	June 20	*c*	*b*	*b*	*b*	June 20	*c*	*b*
1525	--	July 5	*c*	6.4	*b*	*b*	July 5	*c*	*b*
1526	♂	June 27	*c*	5.8	10.7	*b*	June 27	*c*	*b*
*1527	--	June 25	*c*	*b*	*b*	*b*	June 25	*c*	*b*
1528	♂	June 20	*c*	*b*	*b*	*b*	June 20	*c*	*b*
1529	--	July 3	*c*	*b*	*b*	*b*	July 3	*c*	*b*
1530	♂	July 2	*c*	3.1	5.7	2.8	July 2	*c*	2.8
1531	--	July 2	*c*	3.6	6.0	*b*	July 2	*c*	*b*
1532	--	June 30	*c*	4.6	*c*	*b*	June 30	*c*	*b*
*1533[6]	--	July 4	*c*	4.0	8.1	3.8	July 4	*c*	3.9
*1534	♂	July 2	*c*	*b*	*b*	*b*	July 2	*c*	*b*
1535	♂	June 30	*c*	4.6	7.4	4.4	June 30	*c*	*b*
1536	--	June 30	*c*	*b*	6.0	*b*	June 30	*c*	*b*
1537	♂	July 7	*d*	6.1	11.2	6.4	July 7	*d*	6.4
1538	--	June 25	*c*	*b*	*b*	*b*	June 25	*c*	*b*
*1539	--	July 5	*c*	4.6	8.2	4.4	July 5	*c*	4.4
1540	--	July 1	*c*	*b*	*b*	*b*	July 1	*c*	*b*
*1541	♂	June 29	*c*	*b*	*b*	*b*	June 29	*c*	*b*
1542	--	June 27	*c*	*b*	*b*	*b*	June 27	*c*	*b*
1543	♂	July 2	*c*	*b*	*b*	*b*	July 2	*c*	2.8
1544	♂	July 5	*c*	*b*	*b*	*b*	July 5	*c*	*b*
*1545	♂	July 3	*c*	3.2	5.8	*b*	July 3	*c*	*b*
1546	--	June 25	*c*	*b*	*b*	*b*	June 25	*c*	*b*
*1547	--	July 1	*c*	3.1	5.6	*b*	July 1	*c*	*b*
1548	--	July 2	*c*	*b*	5.8	*b*	July 2	*c*	2.8
1549	--	July 9	*d*	4.1	7.2	3.8	July 9	*d*	3.9
*1550[7]	♂	June 30	*c*	5.3	8.4	4.4	June 30	*c*	4.5
1551	♂	July 7	*c*	*b*	*b*	*b*	July 7	*c*	*b*
1552	--	July 3	*c*	4.6	8.1	4.4	July 3	*c*	4.4
1553	--	June 29	*c*	3.0	5.5	*b*	June 29	*c*	*b*
1554	--	July 1	*c*	*b*	*b*	*b*	July 1	*c*	*b*
1555	♂	July 11	*c*	4.5	7.9	*b*	July 11	*c*	*b*
1556	--	July 4	*c*	3.1	5.6	*b*	July 4	*c*	*b*
1557	--	June 28	*c*	3.1	*b*	*b*	June 28	*c*	*b*

[5] 1426. June 25, left chela (probably regenerated) is smaller than right; third right walking-leg missing.

[6] 1533. Plane of removal not at breaking joint.

[7] 1550. Not the same species as majority.

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TABLE I.—*Table of data*—Continued.

Catalog No.	Sex.	Original.							
		Date.	Desc.	Cephalo-thorax.		Left chela.	Right chela.		
				Lg.	Width.		Date.	Desc.	Lg.
1558	--	July 1	*c*	*b*	*b*	*b*	July 1	*c*	*b*
1559	♂	July 8	*d*	6.2	11.3	6.3	July 8	*d*	6.3
*1560	--	[8]July 9	[8]*c*	6.1	11.4	6.1	July 9	*c*	6.2
1561	♂	June 25	*c*	6.1	11.1	6.3	June 25	*c*	6.2
1562	♂	July 2	*c*	4.6	8.6	*b*	July 2	*c*	*b*
*1563	♂	July 1	*c*	*b*	11.6	6.2	July 1	*c*	6.2
1564	--	June 30	*c*	3.6	5.7	3.2	June 30	*c*	3.2
*1565[9]	♂	July 4	*c*	5.1	*b*	4.8	July 4	*c*	4.9
1566	--	June 25	*c*	5.9	11.1	6.1	June 25	*c*	6.3
1567	♂	June 25	*c*	*b*	*b*	*b*	June 25	*c*	*b*
1568	--	June 26	*c*	*b*	8.6	4.5	June 26	*c*	*b*
*1569	--	July 5	*c*	*b*	*b*	*b*	July 5	*c*	*b*
*1570	♂	June 29	*c*	4.0	8.4	*b*	June 29	*c*	*b*
1571	--	July 2	*c*	3.9	6.2	*b*	July 2	*c*	*b*
*1572	--	July 2	*c*	*b*	6.0	*b*	July 2	*c*	*b*
1573	--	June 28	*c*	3.4	5.4	*b*	June 28	*c*	*b*
1574	--	July 17	*d*	*b*	*b*	*b*	July 17	*d*	*b*
1575	♂	July 1	*c*	2.6	3.8	*b*	July 1	*c*	*b*
1576	--	July 6	*c*	3.0	5.4	*b*	July 6	*c*	2.7
*1577	♂	July 2	*c*	2.8	3.7	*b*	July 2	*c*	*b*
1578	--	July 1	*c*	3.2	6.0	2.9	July 1	*c*	2.8
1579	--	June 25	*c*	*b*	*b*	*b*	June 25	*c*	*b*
1580	♂	July 2	*c*	*b*	*b*	*b*	July 2	*c*	*b*
1581	--	June 30	*c*	3.0	5.5	*b*	June 30	*c*	*b*
1582	--	June 26	*c*	3.1	5.8	*b*	June 26	*c*	*b*
*1583	--	[10]July 7	*d*	4.5	7.9	4.3	July 7	*d*	4.4
1584	♂	July 7	*c*	4.4	*b*	4.1	July 7	*c*	4.2
1585	♂	June 25	*c*	*b*	*b*	*b*	June 25	*c*	*b*
1586	--	June 29	*c*	*b*	5.6	*b*	June 29	*c*	*b*
1587	♂	July 1	*c*	*b*	*b*	*b*	July 1	*c*	*b*
*1588	♂	June 30	*c*	4.6	8.2	*b*	June 30	*c*	*b*
1589	♂	June 27	*c*	3.2	5.8	*b*	June 27	*c*	*b*
1590	♂	June 24	*c*	3.1	5.9	2.8	June 24	*c*	2.9
*1591	♂	June 24	*c*	4.8	9.0	5.0	June 24	*c*	5.0
*1592[11]	♂	June 24	*c*	3.3	5.4	3.1	June 24	*c*	3.1
1593	♂	June 24	*c*	4.7	8.5	*b*	June 24	*c*	4.9
1594	--	June 24	*c*	2.8	3.8	*b*	June 24	*c*	*b*
1595	--	June 24	*c*	4.8	8.5	*b*	June 24	*c*	*b*
1596	--	June 24	*c*	*b*	*b*	*b*	June 24	*c*	*b*
1597	♂	June 24	*c*	4.7	8.7	4.7	June 24	*c*	4.7
*1598	♂	June 24?	*c*	*b*	*b*	*b*	June 24	*c*	*b*
*1599[12]	♂	June 24	*c*	2.4	*b*	*b*	June 24	*c*	*b*
1600	--	June 24	*c*	*b*	*b*	*b*	June 24	*c*	4.9
*1601	♂	June 23	*c*	3.2	5.6	*b*	June 23	*c*	*b*
1602	♂	June 23	*c*	3.1	*b*	*b*	June 23	*c*	*b*
1603	♂	July 12	*c*	4.9	8.6	4.9	July 12	*c*	4.9
1604	♂	June 30	*c*	5.0	8.9	4.9	June 30	*c*	*b*
1605	♂	June 27	*c*	4.6	8.2	4.3	June 27	*c*	4.4
1606	♂	July 2	*c*	*b*	*b*	*b*	July 2	*c*	*b*
1607	♂	June 27	*c*	*b*	*b*	*b*	June 27	*c*	*b*
*1608[13]	♂	June 26	*c*	*b*	*b*	*b*	June 26	*c*	*b*

[8] 1560. Died in molting.
[9] 1565. Not the same species as majority.
[10] 1583. Died in molting.
[11] 1592. July 7, first regeneration, removal not at breaking joint; fourth molt = July 31, *k*, 6.8, 12.2, 6.8; July 30, 3d, 4.5.
[12] 1599. Not the same species as the majority; fourth molt = July 31, *k* and *m*, 4.5, 7.2, 4.0; July 31, 3d, 2.9.
[13] 1608. Record not clear; time of original operation not given.

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TABLE 1.—*Table of data*—Continued.

Catalog No.	Sex.	Original.							
		Date.	Desc.	Cephalo-thorax.		Left chela.	Right chela.		
				Lg.	Width.		Date.	Desc.	Lg.
*1609	♂	June 30	*c*	4.5	7.6	*b*	June 30	*c*	*b*
1610	♂	July 3	*c*	5.0	9.0	*c*	July 3	*b*	*b*
1611	--	July 12	*c*	*b*	*b*	*b*	July 12	*c*	*b*
1612	♂	July 7	*c*	*b*	*b*	*b*	July 7	*c*	*b*
*1613[14]	♂	June 29	*c*	3.0	5.4	*b*	June 29	*c*	*b*
*1614	--	July 3	*c*	3.0	5.2	*b*	July 3	*c*	*b*
*1615	--	June 26	*c*	3.0	5.4	*b*	June 26	*c*	*b*
1616	♂	June 25	*c*	*b*	*b*	*b*	June 25	*c*	*b*
*1617	♂	June 27	*c*	4.6	8.1	4.4	June 27	*c*	4.4
*1618	--	June 30	*c*	*b*	*b*	*b*	June 30	*c*	*b*
*1619[15]	--	June 26	*c*	4.6	7.8	*b*	June 26	*c*	4.5
*1620	♂	June 28	*c*	2.9	3.9	*b*	June 28	*c*	*b*
*1621	♂	June 28	*c*	*b*	*b*	*b*	June 28	*c*	*b*
*1622	--	July 8	*c*	2.9	5.3	*b*	July 8	*c*	*b*
1623	--	June 27	*c*	2.9	5.3	*b*	July 8	*c*	*b*
*1624	--	June 28	*c*	3.1	5.8	*b*	June 24	*c*	*b*
1625	--	July 12	*d*	3.0	5.7	2.7	July 12	*d*	2.7
1626	♂	June 29	*c*	3.1	5.4	*b*	June 29	*c*	*b*
1627	♂	July 6	*c*	4.7	8.5	4.4	July 6	*c*	4.6
*1628	♂	July 6	*c*	4.5	8.3	*b*	July 6	*c*	4.4
*1629	♂	June 27	*c*	4.5	*b*	*b*	June 27	*c*	*b*
1630	--	July 14	*c*	4.0	7.0	3.8	July 14	*c*	3.8
1631	--	July 4	*c*	*b*	*b*	4.1	July 4	*c*	*b*
1632	♂	June 25	*c*	*b*	*b*	*b*	June 25	*c*	*b*
*1633	--	June 24	*c*	3.2	5.9	*b*	June 24	*c*	*b*
1634	♂	June 27	*c*	*b*	*b*	*b*	June 27	*c*	*b*
*1635	--	June 23	*c*	*b*	*b*	*b*	June 23	*c*	*b*
*1636	♂	June 27	*c*	5.9	10.7	5.8	June 27	*c*	5.9
*1637	♂	June 29	*c*	*b*	*b*	*b*	June 29	*c*	*b*
*1638	--	July 5	*c*	3.8	7.6	*b*	July 5	*c*	3.6
*1639[16]	--	June 28	*c*	3.0	5.7	*b*	June 28	*c*	*b*
*1640[17]	♂	June 24	*c*	*b*	*b*	*b*	June 24	*c*	*b*
1641	--	June 25	*c*	4.7	8.5	*b*	June 25	*c*	*b*
*1642	--	June 28	*c*	*b*	*b*	*b*	June 28	*c*	*b*
*1731	--	July 1	*c*	4.5	8.7	*b*	July 1	*c*	*b*
1732	--	July 3	*c*	*b*	*b*	*b*	July 3	*c*	*b*
1733	--	July 11	*c*	*b*	*b*	*b*	July 11	*c*	*b*

[14] 1613. June 30, left chela (probably regenerated) smaller than right.

[15] 1619. June 27, right chela (probably regenerated) larger than left, 4th left walking-leg absent; July 5, both chelæ regenerated and of equal size; July 6, right chela (first regeneration) removed; July 21, right chela = small regenerating bud, left chela removed; July 27, both chelæ absent.

[16] 1639. June 29. Right chela (probably regenerated) smaller than left, 2d, 3d, and 4th right walking-legs missing; July 20, right chela smaller than left; July 27, both chelæ present.

[17] 1640. June 25, 2d and 3d left and 2d, 3d, 4th, and 5th right walking-legs missing.

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TABLE I.—*Table of data*—Continued.

Catalog No.	Sex.	First molt. Date.	Desc.	Cephalo-thorax. Lg.	Cephalo-thorax. Width.	Left chela.	Right chela. Date.	Right chela. Desc.	Right chela. Lg.
1394	--	July 4	*c*	3.9	6.2	*b*	June 26	1st	2.8
1397	♂	July 9	*c*	4.3	7.7	4.1	July 9	*c*	4.1
*1398	♂	July 5	*c*	*b*	*b*	*b*	June 25	1st	[18]2.9
1399	♂	July 11	*c*	3.9	7.0	3.8	July 11	*c*	3.9
*1400	♂	July 6	*c*	6.3	*b*	*b*	July 6	*c*	6.5
*1401	--	July 10	*c*	5.6	10.0	*b*	June 29	*o*	5.7
*1402	--	July 11	*c*	*b*	9.8	5.4	June 28	1st	4.6
*1403	♂	July 22	*c*	6.8	12.3	6.7	July 8	[19]1st	5.4
1404	♂	July 12	*c*	5.9	9.2	5.8	July 12	*c*	5.8
1405	♂	July 17	*c*	6.2	11.4	6.3	July 8	*o*	6.3
1406	♂	July 8	*c*	5.6	10.8	5.8	June 25	*o*	5.8
*1407	♂	July 8	*c*	7.3	13.9	7.9	June 25	*o*	7.4
*1408	--	June 26	*c*	*b*	*b*	6.3	June 19	1st	
*1409	♂	July 9	*c*	7.9	15.0	8.1	July 9	*c*	8.4
1410	♂	July 13	*c*	7.4	13.7	7.6	June 30	1st	7.2
1411	♂	July 12	*c*	7.9	14.7	8.1	June 27	*o*	8.5
1412	♂	July 18	*c*	8.0	14.8	8.7	July 3	*o*	8.8
1413	♂	July 9	*c*	7.8	14.3	8.2	June 25	*o*	8.3
1414	♂	July 9	*c*	8.3	14.8	8.4	July 9	*c*	*b*
*1415	♂	July 3	*c*	*b*	*b*	8.1	July 3	*c*	*b*
*1416	♂	July 11	*c*	8.2	14.9	8.2	July 11	*c*	8.5
*1417	♂	July 10	*c*	*b*	*b*	10.2	July 10	*c*	10.4
*1418	♂	July 8	*c*	*b*	17.3	9.3	June 20	1st	
1419	♂	July 8	*c*	7.4	13.6	8.3	June 25	*o*	8.4
*1420	♂	July 11	*c*	*b*	*b*	[20]11.0	July 11	*c*	[20]11.0
1421	♂	July 23	*c*	10.1	19.0	9.6	July 7	*o*	10.7
1422	♂	July 5	*c*	7.9	14.7	8.2	June 25	*o*	8.6
1423	♂	July 20	*c*	9.7	18.0	9.8	July 6	*o*	10.0
1424	♂	July 22	*d*	11.2	20.7	12.3	July 3	*o*	12.3
1425	♂	July 12	*d*	12.4	23.7	14.5	July 7	*o*	14.5
*1426	♂	July 7	*c*	*b*	*b*	9.5	June 25	*o*	10.3
1427	♂	July 12	*d*	12.3	23.5	14.8	July 2	1st	13.8
1428	♂	July 12	*d*	14.4	26.5	17.0	June 30	*o*	17.3
1508	--	July 8	*d*	4.3	7.6	4.2	June 27	*o*	4.4
1509	--	July 9	*d*	*b*	*b*	*b*	June 26	*o*	4.2
1510	--	July 13	*d*	4.8	8.2	4.4	July 10	*o*	4.5
*1511	--	[21]July 10	*d*	4.3	7.5	*b*	July 10	*b*	4.2
1512	♂	July 27	*c*	5.1	9.2	*b*	July 13	*o*	4.9
1513	--	July 4	*c*	*b*	*b*	4.0	July 4	*c*	4.2
1514	--	July 10	*c*	4.1	7.2	3.7	June 30	*o*	3.8
1515	--	July 8	*d*	4.2	7.4	4.0	June 27	*o*	3.9
1516	--	July 13	*c*	3.8	6.6	3.5	July 2	*o*	3.5
*1517	--	July 9	*c*	4.4	7.7	*b*	June 26	*o*	4.3
*1518	♂	July 11	*c*	3.4	7.1	*b*	July 1	*o*	3.3
*1519	--	[22]July 10	*c*	4.1	7.2	3.9	June 25	*o*	4.1
1520	♂	July 19	*c*	6.7	*b*	6.9	July 7	*o*	6.3
*1521	♂	July 19	*c*	5.4	10.1	5.3	July 8	*o*	5.6
*1522	♂	July 9	*c*	5.7	10.1	5.8	July 1	*o*	6.0
1523	♂	(?)	*c*	*b*	*b*	*b*	June 26	*o*	4.3
1524	♂	July 5	*c*	*b*	*b*	8.6	June 25	*o*	8.6
1525	--	July 17	*c*	7.3	13.2	7.3	July 6	*o*	7.4
1526	♂	July 11	*c*	6.9	12.4	6.8	June 28	*o*	7.0
*1527	--	[23]July 13	*c*	*b*	14.5	6.8	June 26	*o*	6.5
1528	♂	July 6	*c*	*b*	*b*	8.6	July 6	*c*	8.7
1529	--	July 14	*c*	6.6	12.3	6.8	July 4	*o*	7.0
1530	♂	July 21	*c*	*b*	8.6	*b*	July 3	*o*	3.3

[18] 1398. Deformed.
[19] 1403. Better classed as second regeneration.
[20] 1420. Approximate value.
[21] 1511. Died in molting.
[22] 1519. Died in molting.
[23] 1527. Died in molting.

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TABLE I.—*Table of data*—Continued.

Catalog No.	Sex.	First molt.							
		Date.	Desc.	Cephalo-thorax.		Left chela.	Right chela.		
				Lg.	Width.		Date.	Desc.	Lg.
1531	--	July 13	*c*	*b*	*b*	*b*	July 3	*o*	4.1
1532	--	July 13	*c*	*b*	*b*	*b*	July 1	*o*	5.6
*1533	--	July 6	*d*	4.6	9.2	4.3	July 5	*o*	4.4
*1534	♂	July 14	*c*	*b*	*b*	*b*	July 3	*o*	3.4
1535	♂	July 11	*c*	5.3	9.7	5.2	July 1	*o*	5.4
1536	--	July 10	*c*	4.3	7.5	4.0	July 1	*o*	4.2
1538	--	July 9	*d*	6.2	11.3	6.1	June 26	*o*	6.3
*1539	--	[24] July 5	*d*	---	----	----	-------	--	---
1540	--	July 13	*c*	4.4	7.9	*b*	July 2	*o*	4.4
*1541	♂	July 12	*c*	5.4	9.8	5.2	June 30	*o*	5.5
1542	--	July 9	*d*	5.6	10.1	5.6	June 28	*o*	5.7
1543	♂	July 15	*d*	3.5	7.0	3.3	July 3	*o*	3.4
1544	♂	July 18	*c*	5.1	10.9	4.8	July 6	*o*	5.0
*1545	♂	July 15	*c*	3.6	7.5	3.5	July 4	*o*	3.5
1546	--	July 12	*c*	5.7	10.1	5.7	July 12	*c*	5.8
*1547	--	[25] July 22	[25] *c*	*b*	7.3	*b*	July 2	*o*	3.4
1548	--	July 23	*d*	3.6	7.3	3.2	July 3	*o*	3.4
*1550	♂	July 17	*c*	6.3	11.3	*b*	July 1	*o*	5.8
1551	♂	July 25	*c*	6.5	12.6	7.3	July 8	*o*	6.8
1552	--	July 17	*d*	5.2	9.2	5.0	July 4	*o*	5.1
1553	--	July 2	*d*	*b*	*b*	*b*	June 30	*o*	3.2
1554	--	July 11	*c*	*b*	*b*	*b*	July 2	*o*	4.4
1555	♂	July 31	*k*	5.0	9.1	4.7	July 12	*o*	4.9
1556	--	July 19	*d*	3.5	6.8	3.2	July 5	*o*	3.3
1557	--	July 8	*c*	3.5	7.0	3.2	July 8	*c*	3.2
1558	--	July 12	*c*	5.5	10.4	5.6	July 2	*o*	5.6
1561	♂	July 10	*c*	7.3	13.5	7.7	June 26	*o*	7.8
1562	♂	July 15	*c*	*b*	10.3	5.6	July 3	*o*	5.7
*1563	♂	July 17	*c*	6.9	13.4	6.9	July 2	*o*	7.1
1564	--	July 10	*c*	4.2	7.0	4.4	July 1	*o*	4.2
*1565	♂	July 21	*c*	6.4	9.3	6.1	July 5	*o*	5.9
1566	--	July 9	*d*	7.3	13.2	7.4	June 26	*o*	7.6
1567	♂	July 8	*c*	6.0	11.0	*b*	June 26	*o*	6.1
1568	--	July 9	*c*	5.7	10.4	5.9	June 27	*o*	6.0
*1569	--	July 13	*c*	*b*	6.8	*b*	July 6	*o*	3.6
*1570	♂	[26] July 18	*c*	4.7	10.0	4.5	June 30	*o*	4.6
1571	--	July 5	*d*	4.2	7.5	4.1	July 3	*o*	4.1
*1572	--	July 13	*c*	*b*	*b*	*b*	July 3	*o*	4.2
1573	--	July 9	*c*	3.9	6.8	3.8	June 29	*o*	3.8
1575	♂	July 10	*c*	*b*	*b*	*b*	July 2	*o*	2 .9
1576	--	July 31	*k*	3.6	7.0	3.2	July 7	*o*	3.2
*1577	♂	July 13	*c*	3.2	5.2	*b*	July 3	*o*	3.1
1578	--	July 12	*c*	3.7	7.6	3.5	July 2	*o*	3.5
1579	--	July 7	*d*	5.9	10.8	5.8	July 7	*c*	5.9
1580	♂	July 12	*c*	3.4	5.5	3.1	July 3	*o*	3.2
1581	--	July 10	*c*	3.6	7.3	3.2	July 1	*o*	3.4
1584	♂	July 18	*d*	6.7	12.1	6.7	July 8	*o*	5.0
1585	♂	July 11	*c*	5.9	10.7	5.9	July 11	*c*	5.9
1586	--	July 13	*c*	3.8	7.5	3.5	July 13	*c*	3.5
1587	♂	July 10	*c*	3.3	5.4	3.0	July 2	*o*	3.0
1588	♂	July 12	*c*	5.4	10.0	5.5	July 1	*o*	5.6
1589	♂	July 8	*c*	*b*	*b*	*b*	June 28	*o*	3.8
1590	♂	July 8	*c*	*b*	5.7	3.6	July 8	*c*	*b*
*1591[27]	♂	July 10	*c*	6.4	11.7	6.5	June 25	*o*	6.7
*1592	♂	July 6	*c*	*b*	*b*	*b*	June 25	*o*	4.0
1593	♂	July 13	*c*	*b*	*b*	*b*	July 13	*c*	*b*
1594	--	July 9	*c*	3.2	5.7	3.2	June 25	*o*	3.1
1595	--	July 11	*c*	5.6	10.5	5.9	June 25	*o*	6.0

[24] 1539. Died in molting.
[25] 1547. Died in molting.
[26] 1570. Date not certain.
[27] 1591. Curved.

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TABLE I.—*Table of data*—Continued.

Catalog No.	Sex.	First molt.							
		Date.	Desc.	Cephalo-thorax.		Left chela.	Right chela.		
				Lg.	Width.		Date.	Desc.	Lg.
1596	—	July 7	*c*	4.3	7.7	4.1	June 25	*o*	4.2
1597	♂	July 11	*c*	6.3	11.1	6.3	July 11	*c*	6.4
*1598	♂	July 5	*c*	*b*	*b*	*b*	June 26	*o*	4.4
*1599	♂	July 4	*c*	*b*	*b*	*b*	June 25	*o*	2.5
1600	—	July 7	*d*	6.2	11.8	6.6	June 25	*o*	6.8
*1601	♂	July 4	*c*	4.0	8.1	3.8	June 25	*o*	3.8
1602	♂	July 11	*c*	4.1	8.2	3.7	July 11	*c*	3.7
1603	♂	July 28	*c*	5.8	10.3	5.8	July 13	*o*	5.4
1604	♂	July 19	*d*	5.7	10.6	5.8	July 1	*o*	5.3
1605	♂	July 13	*c*	5.7	10.7	5.8	June 28	*o*	5.8
1606	♂	July 14	*c*	4.5	8.4	4.8	July 3	*o*	4.2
1607	♂	June 12	*c*	5.9	10.9	5.9	July 12	*c*	5.9
*1608	♂	July 12	*c*	5.8	10.7	*b*	June 27	1st	5.0
*1609	♂	July 30	*c*	*b*	*b*	*b*	July 1	*o*	5.3
1610	♂	July 18	*c*	5.8	10.6	*b*	July 4	*o*	5.8
1611	—	July 29	*c*	5.6	10.1	*b*	July 13	*o*	5.5
1612	♂	July 21	*c*	*b*	*b*	5.0	July 8	*o*	5.0
*1613	♂	July 16	*d*	3.5	6.9	2.7	June 30	*o*	3.3
*1614	—	July 13	*c*	*b*	*b*	*b*	[28]July 4	*o*	2.9
*1615	—	July 13	*d*	3.5	6.8	3.1	[29]June 27	*o*	*b*
1616	♂	July 8	*c*	*b*	11.2	6.0	June 26	*o*	6.1
*1617	♂	July 12	*c*	5.2	9.2	5.0	June 28	*o*	5.3
*1618	—	July 14	*c*	6.4	12.0	5.8	July 1	*o*	5.5
*1619	—	July 5	*c*	*b*	*b*	4.9	June 27	*o*	6.1
*1620	♂	July 8	*c*	*b*	*b*	*b*	June 29	*o*	2.9
*1621[30]	♂	July 14	*c*	4.2	7.3	*b*	July 14	*c*	*b*
*1622	—	July 28	*d*	3.4	6.5	3.1	[31]July 9	*o*	2.7
1623	—	July 17	*d*	3.6	7.1	3.3	July 17	*d*	3.4
*1624	—	July 10	*c*	*b*	*b*	2.9	[32]June 29	*o*	3.0
1626	♂	July 12	*c*	3.6	7.0	*b*	July 12	*c*	3.3
1627	♂	July 17	*c*	5.4	10.0	*b*	July 7	*o*	5.5
*1628	♂	July 18	*c*	5.1	9.6	5.2	July 7	*o*	5.2
*1629	♂	July 10	*c*	5.2	9.6	5.2	July 10	*c*	5.3
1630	—	July 17	*d*	4.9	8.0	4.3	July 15	*o*	4.4
1631	—	July 15	*d*	5.2	8.8	4.7	July 5	*o*	4.8
1632	♂	July 12	*c*	*b*	*b*	*b*	July 12	*c*	*b*
*1633	—	July 3	*c*	4.0	8.0	3.7	June 25	*o*	3.6
1634	♂	July 9	*c*	5.5	*b*	*b*	July 9	*c*	4.8
*1635	—	July 12	*c*	3.9	8.0	3.7	June 25	*o*	3.8
*1636	♂	July 12	*c*	6.9	13.7	7.5	July 12	*c*	*b*
*1637	♂	July 11	*c*	*b*	*b*	*b*	July 11	*c*	*b*
*1638	—	July 31	*k*	4.5	9.0	[33]3.6	July 6	*o*	4.2
*1639	—	(?)	*c*	*b*	*b*	*b*	June 29	*o*	2.6
*1640	♂	July 2	*c*	*b*	*b*	*b*	June 25	*o*	6.9
1641	—	July 8	*c*	5.4	10.2	6.4	July 8	*c*	6.6
*1642	—	July 13	*c*	7.2	12.7	7.5	June 29	*o*	7.5
*1731	—	July 12	*c*	*b*	*b*	6.6	July 2	*o*	6.6
1733	—	July 14	*c*	*b*	7.0	3.8	July 4	*o*	3.9
1733	—	July 24	*c*	5.1	9.8	5.4	July 12	*o*	5.5

[28] 1614. July 4, right chela (probably regenerated) smaller than left.
[29] 1615. Right chela and third right walking-leg missing.
[30] 1621. Curved.
[31] 1622. Date not certain.
[32] 1624. Breaking plane ragged.
[33] 1638. July 6, both chelæ removed, left (probably regenerated) is smaller than right; July 27, both chelæ absent.

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TABLE I.—*Table of data*—Continued.

Catalog No.	Sex.	Second molt.							
		Date.	Desc.	Cephalo-thorax.		Left chela.	Right chela.		
				Lg.	Width		Date.	Desc.	Lg.
1394	--	July 6	*d*	4.0	7.0	3.9	July 5	2d	3.0
1397	♂	July 21	*c*	4.7	8.6	*b*	July 10	*o*	*b*
*1398	♂	July 21	*c*	4.7	8.2	4.5	July 6	2d	3.3
1399	♂	July 19	*d*	4.5	7.6	4.1	July 12	*o*	4.1
*1400	♂	July 20	*c*	7.3	14.0	7.7	July 7	*o*	7.8
*1401	--	[34] July 24	*c*	6.6	11.7	6.6	July 11	1st	5.0
*1402	--	July 31	*c*	6.0	11.1	5.9	July 12	2d	(35)
*1403	♂	July 31	*k*	7.3	13.7	7.4	July 23	[36]2d	5.7
1404	♂	July 31	*k*	6.7	12.2	6.5	July 13	*o*	6.7
1405	♂	July 31	*k*	7.4	13.2	7.4	July 18	1st	6.1
*1406	♂	July 22	*c*	6.4	12.0	6.5	July 9	1st	5.1
*1407	♂	July 24	*c*	8.6	15.8	9.1	July 9	1st	7.7
1408	--	July 11	*c*	7.1	13.5	7.2	June 27	[37]1st	6.7
*1409	♂	July 23	*c*	9.1	17.1	9.6	July 10	*o*	9.6
1410	♂	July 27	*c*	*b*	*b*	*b*	July 14	2d	7.3
1411	♂	July 30	*c*	*b*	*b*	9.6	July 13	1st	7.6
1412	♂	July 31	*k*	9.0	16.2	9.5	July 19	1st	6.0
1413	♂	July 27	*c*	*b*	*b*	*b*	July 10	1st	7.8
1414	♂	July 29	*c*	9.2	16.9	9.2	July 10	*o*	9.4
*1415	♂	July 20	*c*	8.8	15.9	9.6	July 4	[38]1st	8.1
*1416	♂	July 28	*c*	*b*	*b*	*b*	July 12	*o*	10.0
*1417	♂	[39] July 29	*c*	11.0	21.3	12.1	July 11	*o*	12.3
*1418	♂	July 28	*c*	9.7	19.4	10.8	July 9	[40]1st	9.7
1419	♂	July 24	*c*	9.1	16.1	9.3	July 9	1st	8.3
*1420	♂	July 29	*c*	12.7	24.0	14.3	July 12	*o*	14.6
1421	♂	July 31	*k*	11.6	21.9	11.2	July 24	1st	10.3
1422	♂	July 23	*c*	9.1	16.7	9.4	July 6	1st	8.2
1423	♂	July 31	*k*	11.0	20.6	11.4	July 21	1st	9.4
*1426	♂	July 24	*c*	*b*	20.6	11.2	July 8	1st	10.2
1512	♂	July 31	*k*	5.6	10.3	5.5	July 28	1st	3.9
1513	--	July 12	*d*	4.7	7.9	4.4	July 5	*o*	4.5
1514	--	July 24	*c*	4.6	8.5	4.4	July 11	1st	3.6
1516	--	July 28	*d*	4.2	7.2	3.8	July 14	1st	2.9
*1517	♂	[41] July 24	*d*	5.1	9.1	5.0	July 10	1st	3.8
*1518	♂	July 25	*c*	*b*	8.6	*b*	July 12	[42]1st	2.5
1520	♂	July 20	*d*	*b*	*b*	7.5	July 20	1st	5.9
*1521	♂	July 31	*k*	6.1	11.1	6.1	July 20	[43]1st	3.8
*1522	♂	July 24	*c*	6.5	11.6	*b*	July 10	[44]1st	4.6
1523	♂	July 21	*c*	6.2	11.0	6.2	July 21	*c* 1st	5.4
1524	♂	July 22	*c*	9.2	16.6	9.7	July 6	1st	8.4
1525	♂	July 31	*k*	8.5	15.2	8.5	July 18	1st	6.8
1526	♂	July 26	*c*	7.8	13.8	7.6	July 12	1st	6.2
1528	♂	July 21	*c*	9.6	17.7	10.1	July 7	*o*	10.1
1529	--	July 28	*c*	7.7	14.7	8.3	July 15	1st	6.7
1530	♂	July 31	*k*	5.0	9.8	4.6	July 22	1st	4.0
1531	--	July 20	*d*	4.6	8.4	4.4	July 14	1st	3.8
1532	--	July 24	*c*	6.3	11.1	6.3	July 14	1st	5.2
*1534	♂	July 22	*c*	6.5	11.4	5.4	July 15	[45]1st	*b*
1535	♂	July 31	*k*	5.8	10.8	5.8	July 12	1st	4.4
1536	--	July 26	*d*	4.9	8.6	4.7	July 11	1st	3.9
1540	--	July 26	*d*	5.0	9.2	5.1	July 14	1st	3.8

[34] 1401. Died in molting.
[35] 1402. Deformed.
[36] 1403. Better classed as third regeneration.
[37] 1408. First regeneration extends over two molts.
[38] 1415. Extends over two molts.
[39] 1417. Died in molting.
[40] 1418. First regeneration extends over two molts.
[41] 1517. Died in molting.
[42] 1518. Slightly deformed.
[43] 1521. Deformed.
[44] 1522. Deformed.
[45] 1534. Lost in molting.

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TABLE I.—*Table of data*—Continued.

Catalog No.	Sex.	Second molt.							
		Date.	Desc.	Cephalo-thorax.		Left chela.	Right chela.		
				Lg.	Width		Date.	Desc.	Lg.
*1541	♂	[46]July 25	*c*	6.4	11.6	6.3	July 13	1st	5.5
1544	♂	July 31	*k*	5.9	12.5	5.8	July 19	1st	4.2
*1545	♂	July 28	*c*	4.2	8.4	4.0	July 16	[47]1st	*b*
1546	--	July 13	*d*	*b*	*b*	6.0	-------	--	---
*1550	♂	July 31	*k*	6.8	12.7	6.0	July 18	1st	4.9
1551	♂	July 31	*k*	7.9	14.6	8.1	July 26	1st	6.6
1554	--	July 25	*c*	5.1	9.1	4.9	July 12	1st	4.0
1557	--	July 27	*d*	4.4	8.5	4.0	July 9	*o*	3.5
1558	--	July 13	*d*	*b*	*b*	*b*	July 13	*d*	*b*
1561	♂	July 23	*c*	8.8	15.5	9.1	July 11	1st	8.3
1502	♂	July 31	*k*	6.1	11.3	6.3	July 16	1st	5.2
*1563	♂	July 31	*k*	9.1	16.8	9.2	July 18	[48]1st	*b*
1564	--	July 30	*d*	4.7	8.0	4.5	July 11	1st	3.7
*1565	♂	July 31	*k*	7.6	11.6	7.4	July 22	1st	6.7
1568	--	July 24	*d*	6.9	12.1	6.8	July 10	1st	5.6
*1569	--	July 28	*c*	4.5	7.8	4.3	July 14	1st	3.5
*1572	--	[49]July 30	*c*	4.8	8.6	[50]4.1	July 14	1st	3.8
1573	--	July 28	*d*	4.7	7.6	4.2	July 10	1st	3.2
1575	♂	July 23	*c*	3.9	6.6	*b*	July 11	1st	3.2
*1577	♂	July 26	*c*	3.8	6.4	3.6	July 14	[51]1st	3.1
1578	--	July 31	*k*	4.3	8.8	4.0	July 13	1st	3.0
1580	♂	July 25	*c*	3.9	6.7	3.7	July 13	1st	3.1
1581	--	July 31	*k*	4.3	8.7	3.9	July 11	1st	2.6
1585	♂	July 22	*c*	*b*	*b*	*b*	July 12	*o*	7.0
1586	--	July 15	*d*	*b*	*b*	*b*	July 14	*o*	*b*
1587	--	July 24	*c*	*b*	*b*	*b*	July 11	1st	3.0
*1588	♂	[52]July 26	*c*	6.2	11.4	6.4	July 13	1st	5.3
1589	♂	July 31	*k*	4.4	9.0	4.1	July 9	1st	2.7
1590	♂	July 31	*k*	4.6	9.2	4.1	July 9	*o*	4.1
*1591	♂	July 23	*c*	7.3	13.4	7.5	July 11	1st	6.5
*1592	♂	July 17	*c*	5.0	9.0	4.5	July 7	1st	4.4
1593	♂	July 29	*c*	*b*	*b*	*b*	July 14	*o*	7.6
1594	--	July 22	*c*	3.9	6.8	*b*	July 10	1st	3.1
1595	--	July 31	*k*	6.4	11.7	6.5	July 12	1st	4.7
1596	--	July 21	*c*	4.9	8.8	4.8	July 8	1st	4.0
1597	♂	July 24	*c*	7.2	13.1	7.5	July 12	*o*	7.6
*1598	♂	July 21	*c*	*b*	*b*	*b*	July 6	1st	4.5
*1599	♂	July 15	*c*	3.5	5.1	*b*	July 5	1st	2.6
*1601	♂	July 16	*c*	4.7	9.7	*b*	July 5	1st	3.6
1602	♂	July 31	*k*	4.7	9.9	4.4	July 12	*o*	4.5
1603	♂	July 31	*k*	6.2	11.0	6.0	July 29	1st	4.9
1605	♂	July 15	*d*	6.5	11.8	6.2	July 14	1st	4.6
1606	♂	July 23	*d*	5.0	8.7	4.9	July 15	1st	3.9
1607	♂	July 25	*c*	6.8	13.0	7.0	July 13	*o*	7.0
*1608	♂	July 31	*k*	6.6	12.1	6.6	July 13	2d	5.5
*1609	♂	July 31	*k*	6.4	11.7	6.5	July 31	[53]*k*	5.7
1610	♂	July 31	*c*	6.4	11.6	6.0	July 19	1st	4.5
1612	♂	July 31	*k*	5.7	10.2	5.8	July 22	1st	*b*
*1614	--	July 31	*k*	4.2	8.6	4.0	July 14	1st	2.9
1616	♂	July 21	*c*	7.2	12.9	7.2	July 9	1st	6.6
*1617	♂	July 15	*d*	5.7	[54]9.1	5.7	July 13	1st	4.1

[46] 1541. Died in molting.
[47] 1545. Lost in molting.
[48] 1563. Lost in molting.
[49] 1572. Died in molting.
[50] 1572. Deformed.
[51] 1577. Plane of removal not at breaking joint.
[52] 1588. Left chela lost in molting.
[53] 1609. July 20, right chela slightly smaller than left; July 27, both chelæ present.
[54] 1617. Approximate value.

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TABLE I.—*Table of data*—Continued.

Catalog No.	Sex.	Second molt.							
		Date.	Desc.	Cephalo-thorax.		Left chela.	Right chela.		
				Lg.	Width.		Date.	Desc.	Lg.
*1618	--	July 26	*c*	6.7	*b*	*b*	July 15	[55]1st	4.4
*1619	--	July 20	*c*	7.0	12.2	*b*	July 6	1st	6.0
*1620	♂	July 23	*c*	3.8	6.3	3.4	[56]July 9	1st	2.8
*1621	♂	July 31	*k*	4.9	8.4	4.4	July 15	*o*	*b*
*1624	--	July 12	*d*	4.2	8.4	3.7	July 11	1st	3.8
1626	♂	July 18	*d*	4.0	8.0	3.5	July 13	*o*	3.8
1627	♂	July 29	*c*	*b*	*b*	*b*	July 18	1st	5.3
*1628	♂	July 31	*k*	7.1	12.9	7.1	July 19	[57]1st	*b*
*1629	♂	July 24	*c*	6.2	11.3	6.2	July 11	*o*	6.4
1632	♂	July 22	*c*	*b*	*b*	*b*	July 13	*o*	6.9
*1633	--	July 15	*c*	4.7	9.6	4.4	July 4	1st	3.8
1634	♂	July 22	*c*	*b*	*b*	*b*	July 10	*o*	6.1
*1635	--	[58]July 12	*d*	4.6	9.5	4.3	July 12	1st	3.1
*1636	♂	July 25	*c*	8.7	16.1	8.7	July 13	*o*	8.8
*1637	♂	July 27	*c*	*b*	*b*	*b*	July 12	*o*	6.0
*1639	--	July 28	*d*	4.0	8.4	3.9	July 28	*d*	3.0
*1640	♂	July 19	*c*	*b*	*b*	9.0	July 3	1st	7.1
1641	--	July 31	*k*	6.3	11.2	6.1	July 9	*o*	6.0
*1642	--	July 30	*d*	8.0	14.6	8.4	[59]July 14	1st	*b*
*1731	--	July 24	*c*	6.9	12.9	7.3	July 13	1st	6.1
1732	--	July 31	*k*	4.8	8.3	4.6	July 15	1st	3.8
1733	--	July 31	*k*	5.8	10.0	5.8	July 25	1st	4.0

Catalog No.	Sex.	Third molt.							
		Date.	Desc.	Cephalo-thorax.		Left chela.	Right chela.		
				Lg.	Width.		Date.	Desc.	Lg.
1397	♂	July 31	*k*	5.5	9.8	5.2	July 22	1st	3.3
*1398	♂	July 31	*k*	5.2	8.7	4.6	July 22	3d	3.0
*1400	♂	July 31	*k*	8.6	16.1	8.8	July 21	1st	[60]*b*
1406	♂	July 31	*k*	7.3	13.3	7.4	July 23	2d	5.4
*1407	♂	July 31	*k*	9.8	17.6	10.0	July 25	2d	[61]*b*
1408	--	July 31	*k*	8.0	14.8	8.0	July 12	2d	6.1
*1409	♂	July 31	*k*	10.2	19.1	10.6	July 24	1st	8.6
1410	♂	July 31	*k*	10.0	18.4	9.9	July 28	3d	8.9
1411	♂	July 31	*k*	9.7	18.6	10.1	July 31	2d	7.7
1413	♂	July 31	*k*	10.4	18.9	10.9	July 28	2d	8.8
1414	♂	July 31	*k*	10.0	18.4	9.6	July 30	1st	7.2
*1415	♂	July 31	*k*	9.9	18.0	10.9	July 21	2d	*b*
*1416	♂	July 31	*k*	11.3	21.1	11.8	July 29	[62]1st	*b*
1418	♂	July 31	*k*	11.8	22.1	12.5	July 29	[63]2d	10.0
1419	♂	July 31	*k*	9.9	17.7	10.7	July 25	2d	8.9
*1420	♂	July 31	*k*	14.5	27.7	16.9	July 30	1st	14.4
1422	♂	July 31	*k*	10.2	19.1	10.8	July 24	2d	8.5
*1426	♂	July 31	*k*	13.1	24.7	13.5	July 25	2d	11.4
1514	--	July 31	*k*	5.4	9.2	5.2	July 25	2d	3.7
*1518	♂	July 31	*k*	5.0	10.6	4.8	July 26	2d	3.6
*1522	♂	July 31	*k*	7.3	12.8	7.2	July 25	[64]2d	4.1
1523	♂	July 31	*k*	6.8	12.1	6.9	July 22	2d	6.2
1524	♂	July 31	*k*	10.2	18.5	10.9	July 23	2d	8.9

[55] 1618. Injured.
[56] 1620. Not of same species as majority; July 9, plane of removal not at breaking joint.
[57] 1628. Lost in molting.
[58] 1635. Died in molting.
[59] 1642. Lost in molting.
[60] 1400. Right chela lost in molting.
[61] 1407. Probably lost in molting.
[62] 1416. Lost in molting.
[63] 1418. (?)
[64] 1522. Deformed.

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TABLE I.—*Table of data*—Continued.

Catalog No.	Sex.	Third molt.							
		Date.	Desc.	Cephalo-thorax.		Left chela.	Right chela.		
				Lg.	Width.		Date.	Desc.	Lg.
1526	♂	July 31	*k*	8.9	16.5	9.0	July 27	2d	7.2
1528	♂	July 31	*k*	11.0	20.1	11.8	July 22	1st	9.5
1529	--	July 31	*k*	8.6	16.4	9.3	July 29	2d	7.3
1532	--	July 31	*k*	7.0	12.4	7.0	July 25	2d	5.5
*1534	♂	July 30	*d*	*b*	*b*	*b*	July 23	[65]1st	*b*
*1545	♂	July 31	*k*	4.8	9.7	4.5	July 29	2d	3.0
1554	--	July 31	*k*	5.9	10.8	6.1	July 26	2d	4.4
1561	♂	July 31	*k*	10.2	17.7	10.3	July 24	2d	8.2
*1569	--	July 30	*d*	4.6	8.2	4.5	July 29	[66]2d	(66)
1575	♂	July 31	*k*	4.5	7.8	4.4	July 24	2d	3.6
*1577	♂	July 28	*d*	4.2	7.3	4.3	July 27	[67]2d	3.0
1580	♂	July 31	*k*	4.4	8.1	4.4	July 26	2d	3.8
1585	♂	July 31	*k*	8.0	14.8	8.1	July 23	1st	6.8
1587	♂	July 31	*k*	4.4	7.9	4.3	July 25	2d	3.3
*1588	♂	July 31	*k*	6.9	12.5	[68]*b*	July 27	2d	5.2
*1591	♂	July 31	*k*	8.3	15.3	8.6	July 24	[69]2d	6.9
1592	♂	July 29	*c*	*b*	*b*	*b*	July 18	2d	4.0
1593	♂	July 31	*k*	8.4	15.2	8.8	July 30	1st	6.9
1594	--	July 31	*k*	4.4	7.8	4.1	July 23	2d	3.1
1596	--	July 31	*k*	5.5	9.9	5.5	July 22	2d	3.9
1597	♂	July 31	*k*	8.3	15.4	8.8	July 25	1st	7.6
*1598	♂	July 31	*k*	5.8	10.3	5.7	July 22	[70]2d	*b*
*1599	♂	July 31	*c*	4.0	6.1	3.3	July 16	2d	2.7
*1601	♂	July 31	*k*	5.4	9.0	5.1	July 17	[71]2d	3.2
1607	♂	July 31	*k*	8.3	15.2	8.3	July 26	1st	7.3
1610	♂	July 31	*k*	7.1	13.2	7.1	July 31	2d	5.5
1616	♂	July 31	*k*	8.1	15.1	8.5	July 22	2d	7.0
*1618	--	July 29	*d*	8.3	*b*	8.7	July 27	[72]2d	5.7
*1619	--	July 31	*k*	8.3	14.5	8.3	July 20	2d	*b*
*1620	♂	July 31	*k*	4.4	7.6	4.0	July 24	2d	3.4
1627	♂	July 31	*k*	7.3	13.8	7.7	July 30	2d	6.4
*1629	♂	July 31	*k*	7.0	12.8	7.0	July 25	[73]1st	3.9
1632	♂	July 31	*k*	7.8	14.6	8.2	July 23	1st	6.6
*1633	--	July 17	*d*	5.3	10.8	5.2	July 16	[74]2d	3.8
1634	♂	July 31	*k*	6.9	12.6	6.4	July 23	1st	5.2
*1636	♂	July 31	*k*	10.0	18.9	10.5	July 26	[75]1st	7.9
1637	♂	July 31	*k*	6.8	12.2	6.6	July 28	[76]1st	4.2
*1640	♂	July 31	*k*	9.7	17.7	10.4	July 20	2d	7.1
*1731	--	July 31	*k*	8.0	14.4	8.3	July 25	[77]2d	5.0

[65] 1534. Lost in molting.
[66] 1569. Deformed.
[67] 1577. Deformed.
[68] 1588. Left chela lost in molting.
[69] 1591. Curved.
[70] 1598. Lost in molting.
[71] 1601. Deformed.
[72] 1618. Deformed.
[73] 1629. Chela very stout.
[74] 1633. Curved.
[75] 1636. Deformed.
[76] 1637. Deformed.
[77] 1731. Deformed.

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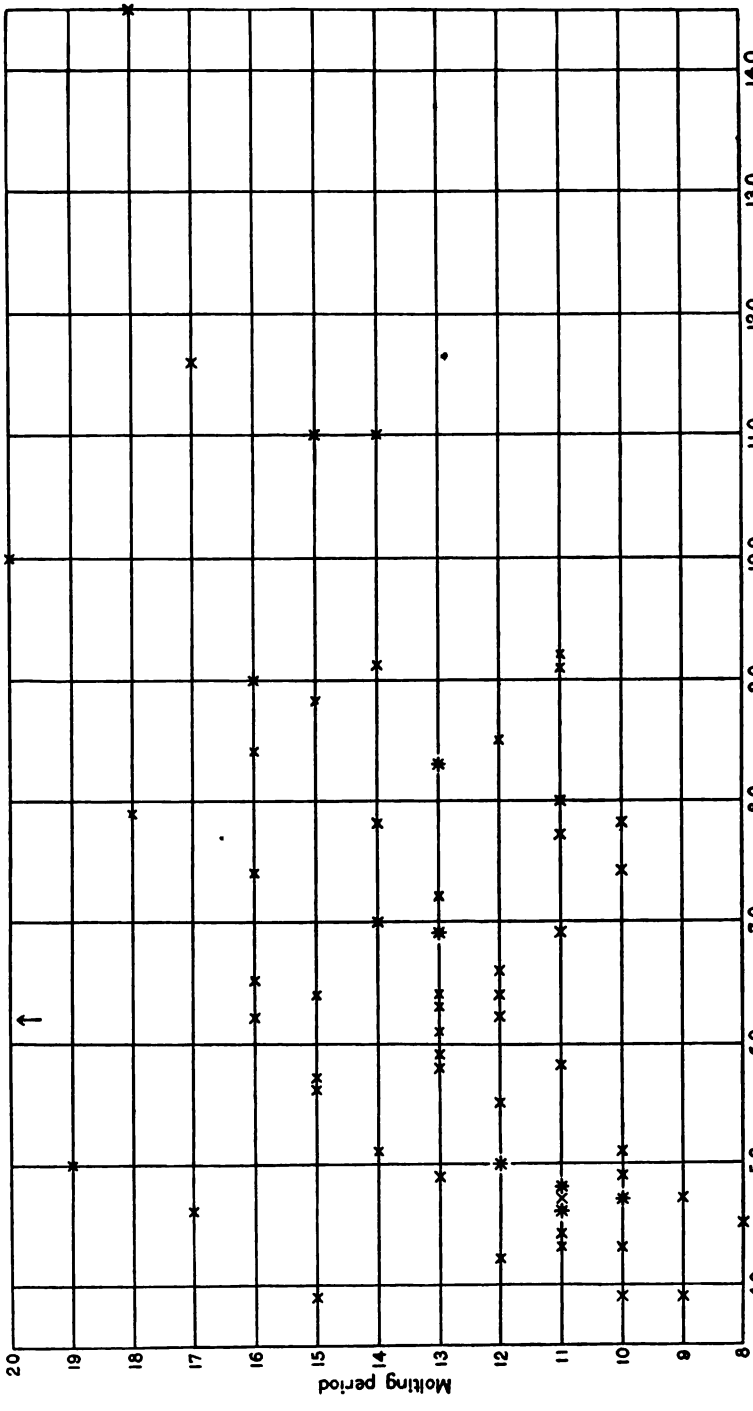

TABLE 2.—Correlation between cephalo-thoracic length and molting period (first regeneration period). • Superposition of two cases.

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TABLE 3.—*Correlation between cephalo-thoracic length and molting period (first regeneration period).*

[Data arranged in order of length of molting period.]

Catalog No.	Molting period.	Cephalo-thoracic length.	Catalog No.	Molting period.	Cephalo thoracic length.	Catalog No.	Molting period.	Cephalo-thoracic length.
1569	8	4.5	1422	11	9.1	1629	14	7.0
1575	9	3.9	1524	11	9.2	1526	14	7.8
1633	9	4.7	1516	12	4.2	1419	14	9.1
1580	10	3.9	1540	12	5.0	1528	14	11.0
1581	10	4.3	1606	12	5.0	1594	15	3.9
1564	10	4.7	1397	12	5.5	1512	15	5.6
1601	10	4.7	1588	12	6.2	1617	15	5.7
1536	10	4.9	1595	12	6.4	1610	15	6.4
1554	10	5.1	1401	12	6.6	1561	15	8.8
1405	10	7.4	1525	12	8.5	1423	15	11.0
1632	10	7.8	1596	13	4.9	1603	16	6.2
1578	11	4.3	1733	13	5.8	1605	16	6.5
1589	11	4.4	1544	13	5.9	1591	16	7.3
1514	11	4.6	1562	13	6.1	1593	16	8.4
1531	11	4.6	1532	13	6.3	1412	16	9.0
1573	11	4.7	1541	13	6.4	1635	17	4.6
1572	11	4.8	1568	13	6.9	1421	17	11.6
1732	11	4.8	1634	13	6.9	1551	18	7.9
1535	11	5.8	1616	13	7.2	1420	18	14.5
1731	11	6.9	1597	13	8.3	1530	19	5.0
1529	11	7.7	1607	13	8.3	1414	20	10.0
1585	11	8.0	1517	14	5.1	1523	25	6.2

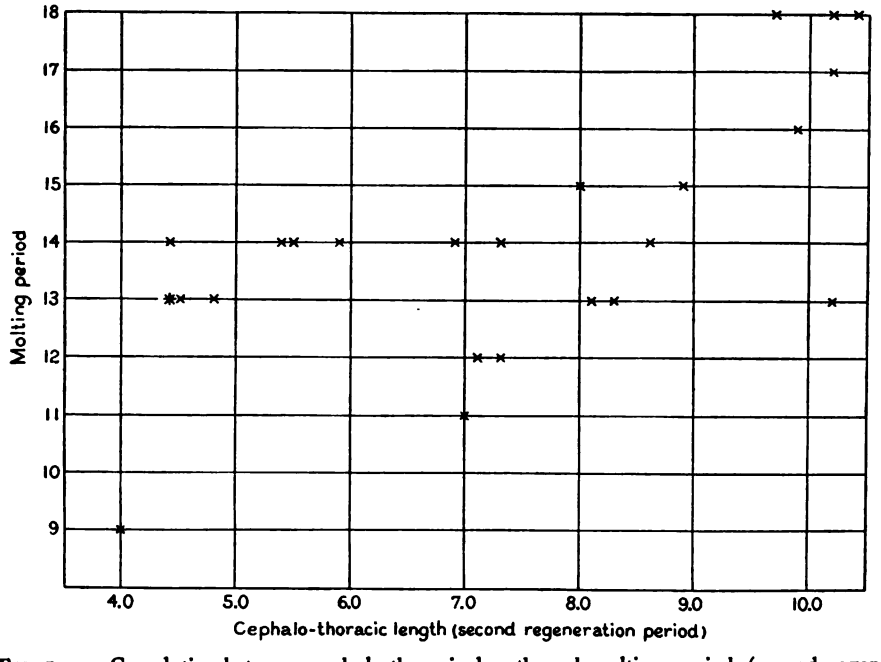

TABLE 4.—Correlation between cephalo-thoracic length and molting period (second regeneration period). * Superposition of two cases.

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TABLE 5.—*Correlation between cephalo-thoracic length and molting period (second regeneration period).*

[Data arranged in order of length of molting period.]

Catalog No.	Molting period.	Cephalo-thoracic length.	Catalog No.	Molting period.	Cephalo-thoracic length.	Catalog No.	Molting period.	Cephalo-thoracic length.
1394	9	4.0	1591	13	8.3	1408	15	8.0
1532	11	7.0	1561	13	10.2	1526	15	8.9
1610	12	7.1	1587	14	4.4	1419	16	9.9
1627	12	7.3	1514	14	5.4	1524	17	10.2
1580	13	4.4	1596	14	5.5	1411	18	9.7
1594	13	4.4	1554	14	5.9	1422	18	10.2
1575	13	4.5	1588	14	6.9	1413	18	10.4
1545	13	4.8	1406	14	7.3			
1616	13	8.1	1529	14	8.6			

TABLE 6.—*Correlation between molting period and amount of first regeneration.*

[Data arranged in order of length of molting period.]

Catalog No.	Molting period.	Right chela, first regeneration.	Catalog No.	Molting period.	Right chela, first regeneration.	Catalog No.	Molting period.	Right chela, first regeneration.
1569	8	3.5	1585	11	6.8	1629	14	3.9
1587	9	3.0	1422	11	8.2	1526	14	6.2
1575	9	3.2	1524	11	8.4	1419	14	8.3
1633	9	3.8	1516	12	2.9	1528	14	9.5
1581	10	2.6	1397	12	3.3	1594	15	3.1
1580	10	3.1	1540	12	3.8	1512	15	3.9
1601	10	3.6	1606	12	3.9	1617	15	4.1
1564	10	3.7	1595	12	4.7	1610	15	4.5
1536	10	3.9	1401	12	5.0	1561	15	8.3
1554	10	4.0	1588	12	5.3	1423	15	9.4
1598	10	4.5	1525	12	6.8	1605	16	4.6
1405	10	6.1	1596	13	4.0	1603	16	4.9
1632	10	6.6	1733	13	4.0	1412	16	6.0
1589	11	2.7	1544	13	4.2	1591	16	6.5
1578	11	3.0	1532	13	5.2	1593	16	6.9
1573	11	3.2	1562	13	5.2	1411	16	7.6
1514	11	3.6	1634	13	5.2	1635	17	3.1
1531	11	3.8	1541	13	5.5	1421	17	10.3
1572	11	3.8	1568	13	5.6	1551	18	6.6
1732	11	3.8	1520	13	5.9	1420	18	14.4
1535	11	4.4	1616	13	6.6	1530	19	4.0
1627	11	5.3	1607	13	7.3	1414	20	7.2
1731	11	6.1	1597	13	7.6	1523	25	5.4
1529	11	6.7	1517	14	3.8			

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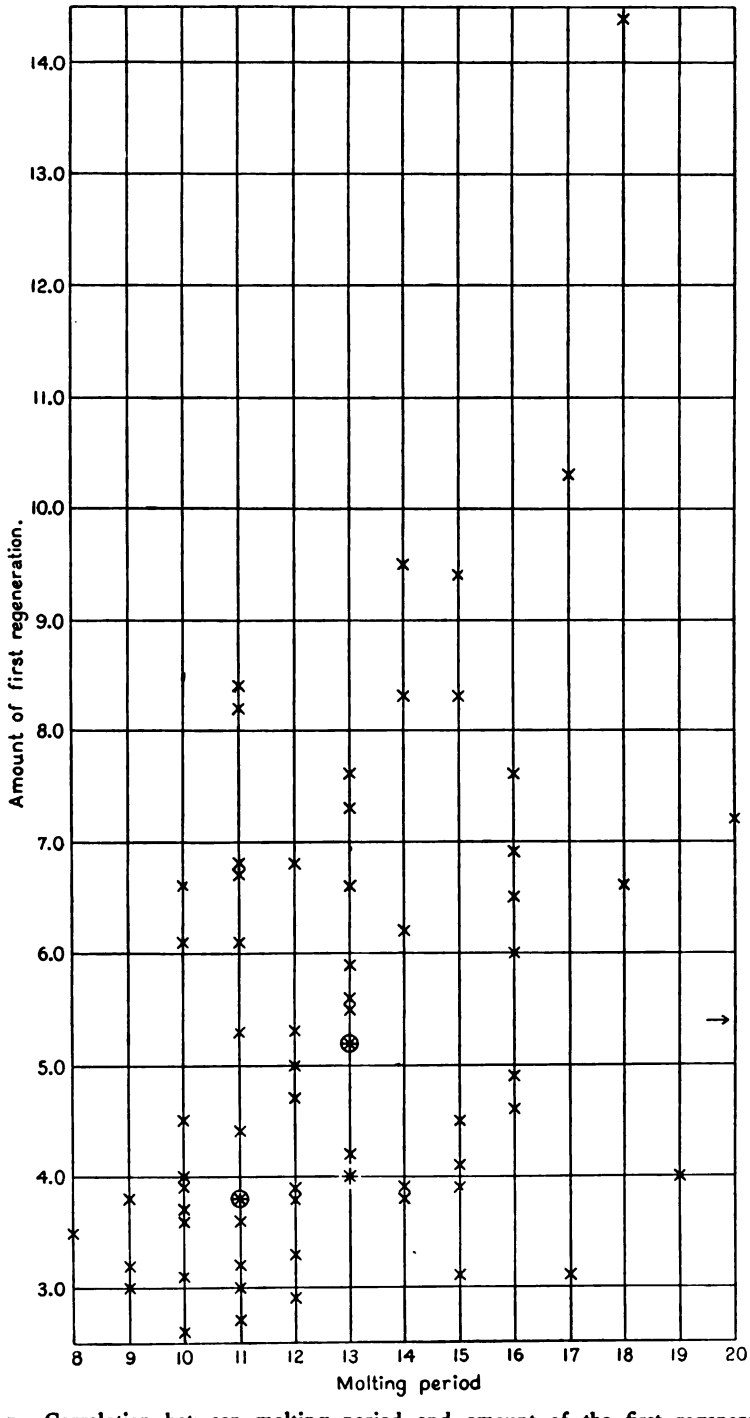

TABLE 7.—Correlation between molting period and amount of the first regeneration of the right chela. * Superposition of two cases; ⊗ Superposition of three cases.

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TABLE 8.—*Correlation between molting period and amount of second regeneration.*

[Data arranged in order of length of molting period.]

Catalog No.	Molting period.	Right chela, second regeneration.	Catalog No.	Molting period.	Right chela, second regeneration.	Catalog No.	Molting period.	Right chela, second regeneration.
1394	9	3.0	1616	13	7.0	1529	14	7.3
1532	11	5.5	1561	13	8.2	1408	15	6.1
1610	12	5.5	1587	14	3.3	1526	15	7.2
1627	12	6.4	1514	14	3.7	1419	16	8.9
1545	13	3.0	1596	14	3.9	1524	17	8.9
1594	13	3.1	1554	14	4.4	1411	18	7.7
1575	13	3.6	1588	14	5.2	1422	18	8.5
1580	13	3.8	1506	14	5.4	1413	18	8.8
1591	13	6.9	1410	14	7.3			

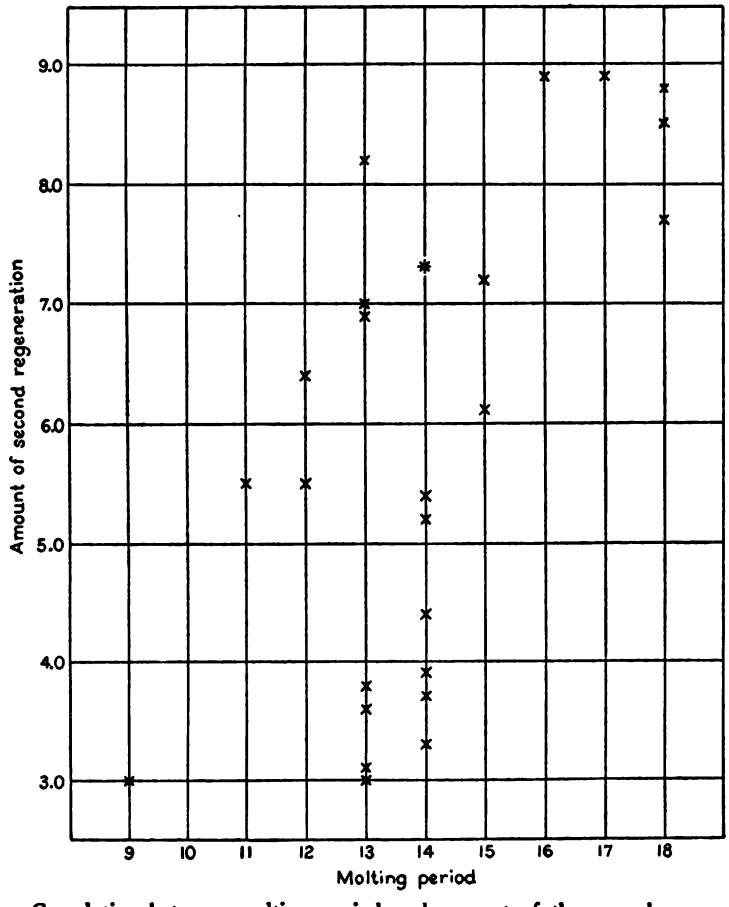

TABLE 9.—Correlation between molting period and amount of the second regeneration of the right chela. * Superposition of two cases.

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TABLE 10.—*Correlation between the cephalo-thoracic length and the amount of the first and second regenerations of the right chela.*

[The specific amount of regeneration is the length of the regenerated chela divided by the cephalo-thoracic length.]

First regeneration				Second regeneration.			
Catalog No.	Specific amount.	Cephalo-thoracic length.	Right chela, first regeneration.	Right chela, second regeneration.	Cephalo-thoracic length.	Specific amount.	Catalog No.
1580	0.795	3.9	3.1				
1594	.795	3.9	3.1				
1575	.821	3.9	3.2	3.0	4.0	0.750	1394
1516	.690	4.2	2.9				
1581	.605	4.3	2.6				
1578	.698	4.3	3.0	3.1	4.4	.705	1594
1589	.614	4.4	2.7	3.3	4.4	.750	1587
1569	.778	4.5	3.5	3.8	4.4	.864	1580
1635	.674	4.6	3.1	3.6	4.5	.800	1575
1514	.783	4.6	3.6				
1531	.826	4.6	3.8				
1573	.681	4.7	3.2				
1601	.766	4.7	3.6				
1564	.787	4.7	3.7				
1633	.809	4.7	3.8				
1572	.792	4.8	3.8	3.0	4.8	.625	1545
1732	.792	4.8	3.8				
1536	.796	4.9	3.9				
1596	.816	4.9	4.0				
1540	.760	5.0	3.8				
1606	.780	5.0	3.9				
1530	.800	5.0	4.0				
1517	.745	5.1	3.8				
1554	.784	5.1	4.0	3.7	5.4	.685	1514
1397	.600	5.5	3.3	3.9	5.5	.709	1596
1512	.696	5.6	3.9				
1617	.719	5.7	4.1				
1733	.690	5.8	4.0				
1535	.759	5.8	4.4				
1544	.712	5.9	4.2	4.4	5.9	.746	1554
1562	.852	6.1	5.2				
1603	.790	6.2	4.9				
1588	.855	6.2	5.3				
1523	.871	6.2	5.4				
1532	.825	6.3	5.2				
1610	.703	6.4	4.5				
1595	.734	6.4	4.7				
1541	.859	6.4	5.5				
1605	.708	6.5	4.6				
1401	.758	6.6	5.0				
1634	.754	6.9	5.2				
1568	.812	6.9	5.6	5.2	6.9	.754	1588
1731	.884	6.9	6.1				
1629	.557	7.0	3.9	5.5	7.0	.786	1532
1616	.917	7.2	6.6	5.5	7.1	.775	1610
1591	.890	7.3	6.5	5.4	7.3	.740	1406
1405	.824	7.4	6.1	6.4	7.3	.877	1627
1529	.870	7.7	6.7				
1526	.795	7.8	6.2				
1632	.846	7.8	6.6				
1551	.835	7.9	6.6				

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TABLE 10.—*Correlation between the cephalo-thoracic length and the amount of the first and second regenerations of the right chela*—Continued.

First regeneration.				Second regeneration.			
Catalog No.	Specific amount.	Cephalo-thoracic length.	Right chela, first regenera-tion.	Right chela, second regenera-tion.	Cephalo-thoracic length.	Specific amount.	Catalog No.
1585	.850	8.0	6.8	6.1	8.0	.762	1408
1607	.880	8.3	7.3	7.0	8.1	.864	1616
1597	.916	8.3	7.6	6.9	8.3	.831	1591
1593	.821	8.4	6.9				
1525	.800	8.5	6.8	7.3	8.6	.849	1529
1561	.943	8.8	8.3	7.2	8.9	.809	1526
1412	.667	9.0	6.0				
1422	.901	9.1	8.2	7.7	9.7	.794	1411
1419	.912	9.1	8.3	8.9	9.9	.899	1419
1524	.913	9.2	8.4	8.2	10.2	.804	1561
1414	.720	10.0	7.2	8.5	10.2	.833	1422
1423	.855	11.0	9.4	8.9	10.2	.873	1524
1528	.864	11.0	9.5	8.8	10.4	.846	1413
1421	.888	11.6	10.3				
1420	.993	14.5	14.4				

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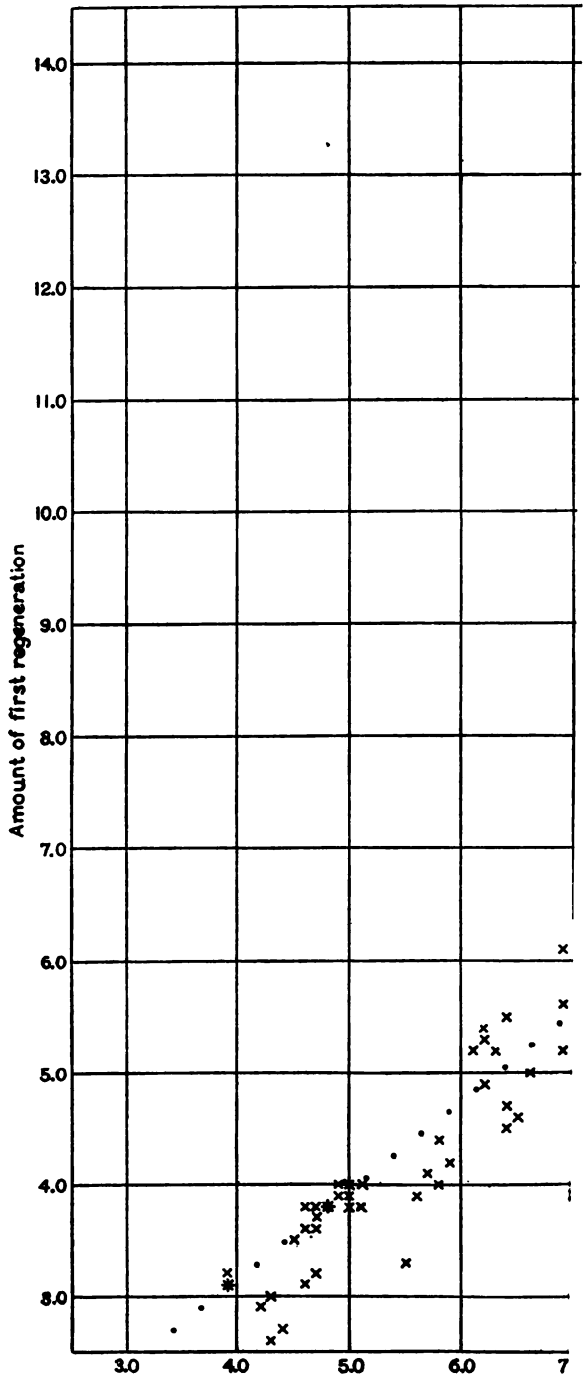

TABLE XIA.—Correlation between cephalo-thoracic length
line, line along which all data would be arran

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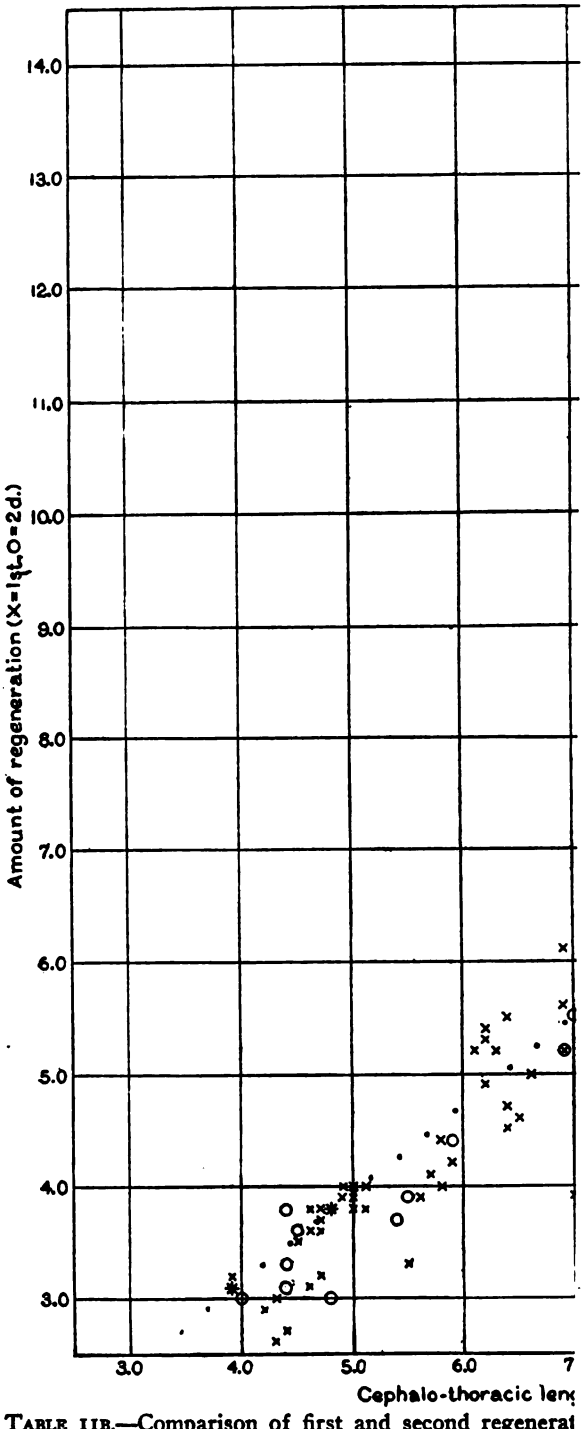

TABLE IIB.—Comparison of first and second regenerat generation; * superposition of two cases of first regeneration.

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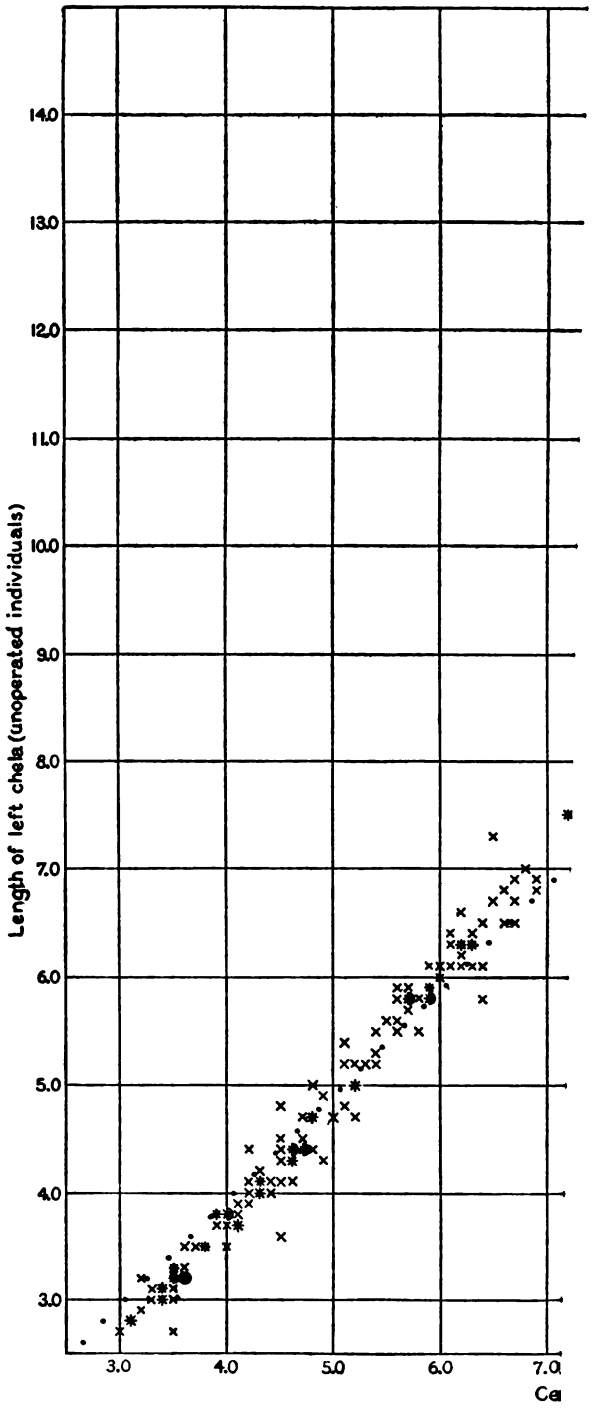

TABLE IIC.—Correlation between left chela-length and t
data would be arranged if specific length of left che
⊗ = 4 cases; arrows = cases which come beyond lin

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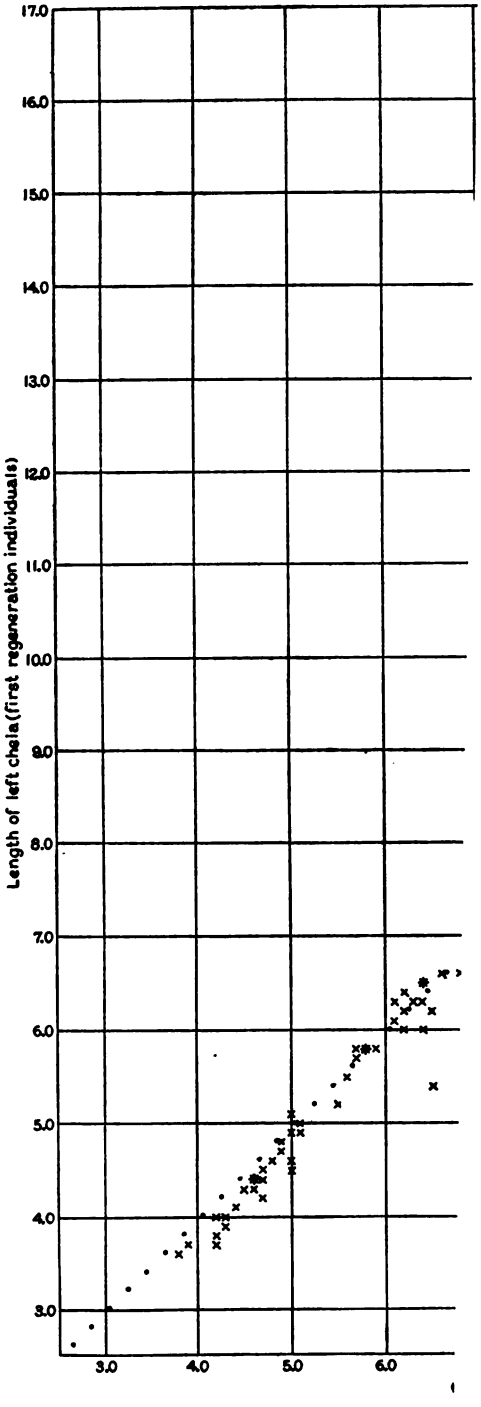

TABLE IID.—Correlation between left ch
line, line along which all the data wc
sizes of individuals. * Superposition

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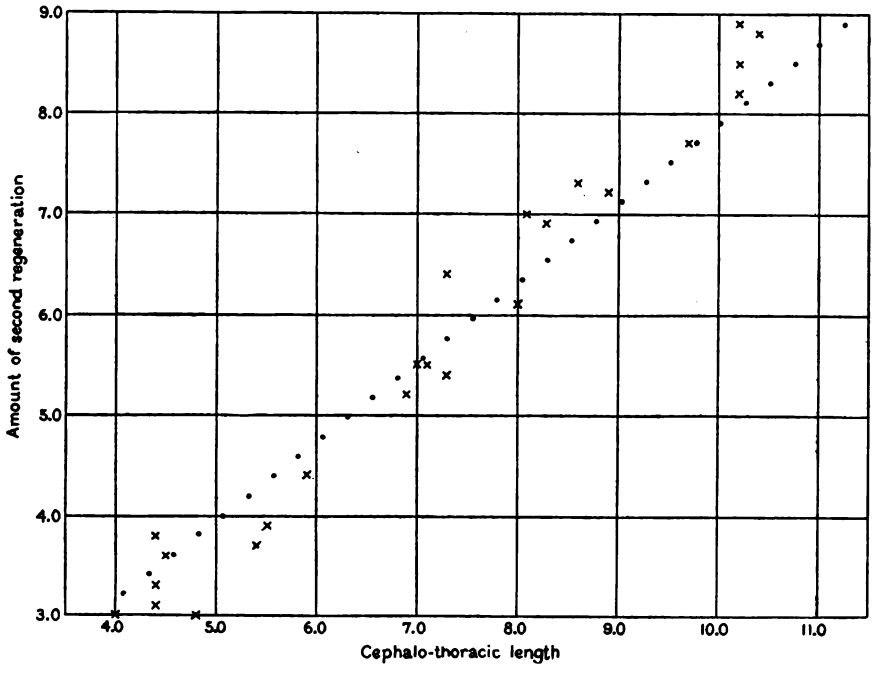

TABLE 12.—Correlation between cephalo-thoracic length and amount of second regeneration of right chela. *Dotted line,* line along which all the data would be arranged if specific amount of regeneration were the same for individuals of all sizes.

TABLE 13.—*Comparisons of the first, second, and third regenerations in single individuals.*

[Data arranged in order of original length of the removed chela.]

Catalog No.	Original length.	First regeneration.	Second regeneration.	Third regeneration.	Catalog No.	Original length.	First regeneration.	Second regeneration.	Third regeneration.
1599	2.5	2.6	2.7	2.9	1588	5.6	5.3	5.2	
1575	2.9	3.2	3.6		1610	5.8	4.5	5.5	
1587	3.0	3.0	3.3		1616	6.1	6.6	7.0	
1594	3.1	3.1	3.1		1410	6.5	(*)	7.3	8.9
1580	3.2	3.1	3.8		1591	6.7	6.5	6.9	
1514	3.8	3.6	3.7		1526	7.0	6.2	7.2	
1596	4.2	4.0	3.9		1529	7.0	6.7	7.3	
1523	4.3	5.4	6.2		1561	7.8	8.3	8.2	
1554	4.4	4.0	4.4		1411	8.5	7.6	7.7	
1627	5.5	5.3	6.4		1524	8.6	8.4	8.9	
1532	5.6	5.2	5.5						

* First regeneration record missing.

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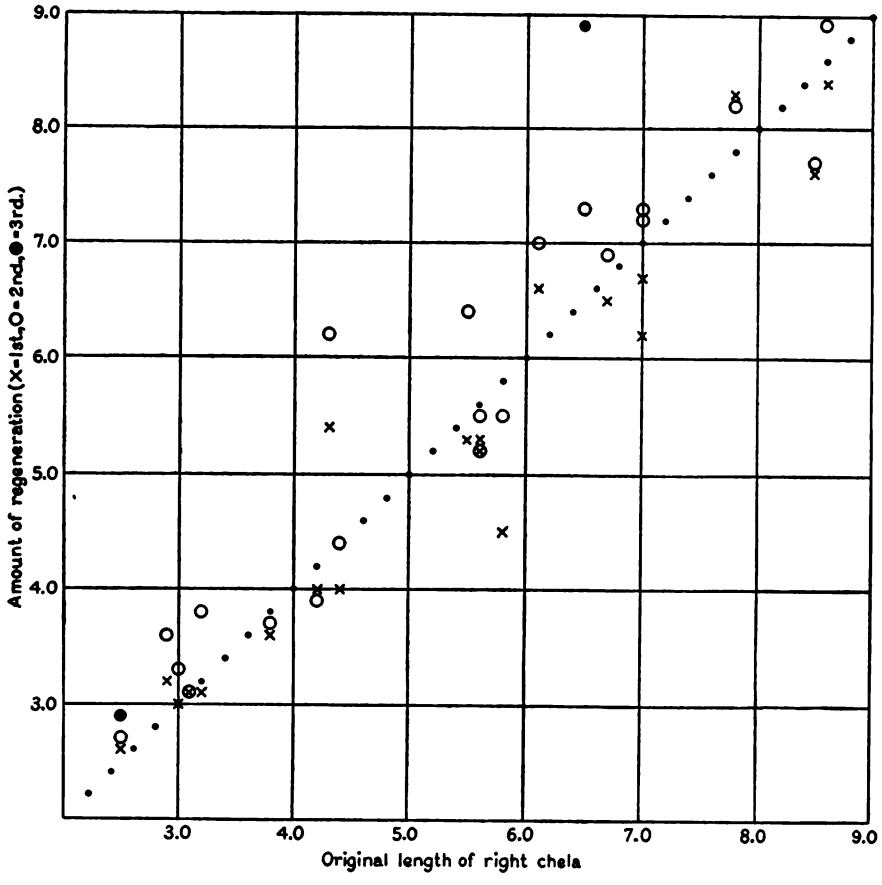

TABLE 14.—Comparisons of first, second, and third regenerations of right chela in single individuals and their correlation with original chela-lengths. *Dotted line,* line along which all the data would be arranged if regenerated chela-lengths were equal to original chela-lengths. × first regeneration; ⊙ second regeneration; ⊗ third regeneration.

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TABLE 15.—*Correlation between the left and right chelæ and the cephalo-thoracic length in unoperated individuals.*

[Data arranged in order of cephalo-thoracic length. Asterisks (*) indicate individuals without catalog numbers, collected especially for these measurements. All of these starred cases, with one exception (* ♀), were males.]

Catalog No.	Cephalo-thoracic length.	Left chela length.	Right chela length.	Ratio of left chela to cephalo-thoracic length.	Catalog No.	Cephalo-thoracic length.	Left chela length.	Right chela length.	Ratio of left chela to cephalo-thoracic length.
1625	3.0	2.7	2.7	0.900	(*)	4.5	4.4	4.5	.978
1530	3.1	2.8	2.8	.903	(*)	4.5	4.5	4.5	1.000
1590	3.1	2.8	2.9	.903	1606	4.5	4.8	4.2	1.067
1578	3.2	2.9	2.8	.906	1590	4.6	4.1	4.1	.891
1594	3.2	3.2	3.1	1.000	1533	4.6	4.3	4.4	.935
1587	3.3	3.0	3.0	.909	1605	4.6	4.3	4.4	.935
1592	3.3	3.1	3.1	.939	1539	4.6	4.4	4.4	.957
(*)	3.4	3.0	3.1	.882	1552	4.6	4.4	4.4	.957
(*)	3.4	3.0	3.1	.882	1617	4.6	4.4	4.4	.957
1580	3.4	3.1	3.2	.912	1513	4.7	4.4	4.5	.936
1622	3.4	3.1	2.7	.912	1602	4.7	4.4	4.5	.936
1613	3.5	2.7	3.3	.771	1627	4.7	4.4	4.6	.936
(*)	3.5	3.0	3.1	.857	1570	4.7	4.5	4.6	.957
(*)	3.5	3.1	3.2	.886	1597	4.7	4.7	4.7	1.000
1556	3.5	3.2	3.3	.914	1510	4.8	4.4	4.5	.917
1557	3.5	3.2	3.2	.914	1402	4.8	4.7	4.8	.979
1394	3.5	3.3	3.3	.943	(*)	4.8	4.7	4.6	.979
1543	3.5	3.3	3.4	.943	1591	4.8	5.0	5.0	1.042
1548	3.6	3.2	3.4	.889	1630	4.9	4.3	4.4	.878
1564	3.6	3.2	3.2	.889	1603	4.9	4.9	4.9	1.000
1576	3.6	3.2	3.2	.889	1555	5.0	4.7	4.9	.940
1581	3.6	3.2	3.4	.889	1544	5.1	4.8	5.0	.941
1623	3.6	3.3	3.4	.917	1628	5.1	5.2	5.2	1.020
1545	3.6	3.5	3.5	.972	1733	5.1	5.4	5.5	1.059
1578	3.7	3.5	3.5	.946	1631	5.2	4.7	4.8	.904
1516	3.8	3.5	3.5	.921	1552	5.2	5.0	5.1	.962
1586	3.8	3.5	3.5	.921	1617	5.2	5.0	5.3	.962
1635	3.9	3.7	3.8	.949	1629	5.2	5.2	5.3	1.000
1399	3.9	3.8	3.9	.974	1535	5.3	5.2	5.4	.982
1573	3.9	3.8	3.8	.974	1541	5.4	5.2	5.5	.963
1626	4.0	3.5	3.8	.875	1521	5.4	5.3	5.6	.981
1633	4.0	3.7	3.6	.925	1588	5.4	5.5	5.6	1.019
1533	4.0	3.8	3.9	.950	1558	5.5	5.6	5.6	1.018
1601	4.0	3.8	3.8	.950	(*)	5.6	5.5	5.6	.982
1630	4.0	3.8	3.8	.950	1542	5.6	5.6	5.7	1.000
1514	4.1	3.7	3.8	.902	1406	5.6	5.8	5.8	1.036
1602	4.1	3.7	3.7	.902	1595	5.6	5.9	6.0	1.054
1549	4.1	3.8	3.9	.927	1546	5.7	5.7	5.8	1.000
1519	4.1	3.9	4.1	.951	1522	5.7	5.8	6.0	1.018
1510	4.2	3.9	3.9	.929	1605	5.7	5.8	5.8	1.018
1515	4.2	4.0	3.9	.952	1604	5.7	5.8	5.3	1.018
1571	4.2	4.1	4.1	.976	1568	5.7	5.9	6.0	1.035
1564	4.2	4.4	4.2	1.048	(*)	5.8	5.5	5.6	.948
1396	4.3	4.0	4.0	.930	1603	5.8	5.8	5.4	1.000
1536	4.3	4.0	4.2	.930	1404	5.9	5.8	5.8	.983
1397	4.3	4.1	4.1	.953	1579	5.9	5.8	5.9	.983
1596	4.3	4.1	4.2	.953	1636	5.9	5.8	5.9	.983
1508	4.3	4.2	4.4	.977	1585	5.9	5.9	5.9	1.000
1557	4.4	4.0	3.5	.909	1607	5.9	5.9	5.9	1.000
1584	4.4	4.1	4.2	.932	1566	5.9	6.1	6.3	1.034
1638	4.5	3.6	4.2	.800	(*)	6.0	6.0	6.1	1.000
1399	4.5	4.1	4.1	.911	1422	6.0	6.1	6.1	1.017
1583	4.5	4.3	4.4	.956	1560	6.1	6.1	6.2	1.000

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TABLE 15.—*Correlation between the left and right chelæ and the cephalo-thoracic length in unoperated individuals*—Continued.

Catalog No.	Cephalo-thoracic length.	Left chela-length.	Right chela-length.	Ratio of left chela to cephalo-thoracic length.	Catalog No.	Cephalo-thoracic length.	Left chela-length.	Right chela-length.	Ratio of left chela to cephalo-thoracic length.
1561	6.1	6.3	6.2	1.033	1561	7.3	7.7	7.8	1.055
1537	6.1	6.4	6.4	1.049	1407	7.3	7.9	7.4	1.082
1538	6.2	6.1	6.3	.984	1419	7.4	8.3	8.4	1.122
1629	6.2	6.2	6.4	1.000	(*)	7.7	7.7	7.8	1.000
1405	6.2	6.3	6.3	1.016	1413	7.8	8.2	8.3	1.051
1559	6.2	6.3	6.3	1.016	1409	7.9	8.1	8.4	1.025
1600	6.2	6.6	6.8	1.065	1411	7.9	8.1	8.5	1.025
(*)	6.3	6.1	6.3	.968	1422	7.9	8.2	8.6	1.038
1597	6.3	6.3	6.4	1.000	(*)	8.0	8.4	8.5	1.050
(*)	6.3	6.3	6.3	1.000	(*)	8.0	8.5	8.7	1.062
(*)	6.3	6.4	6.5	1.016	1412	8.0	8.7	8.8	1.087
1618	6.4	5.8	5.5	.906	1416	8.2	8.2	8.5	1.000
1565	6.4	6.1	5.9	.953	(*)	8.6	8.9	9.1	1.035
1591	6.4	6.5	6.7	1.016	1420	8.6	9.4	9.4	1.093
(*)	6.5	6.7	6.7	1.031	1636	8.7	8.7	8.8	1.000
1551	6.5	7.3	6.8	1.123	1409	9.1	9.6	9.6	1.055
(*)	6.6	6.5	6.7	.985	1414	9.2	9.2	9.4	1.000
1529	6.6	6.8	7.0	1.030	(*)	9.5	9.7	8.9	1.021
1404	6.7	6.5	6.7	.970	1528	9.6	10.1	10.1	1.052
1584	6.7	6.7	5.0	1.000	1423	9.7	9.8	10.0	1.010
1520	6.7	6.9	6.3	1.030	1421	10.1	9.6	10.7	.950
1607	6.8	7.0	7.0	1.029	(*)	10.1	10.0	10.7	.990
1526	6.9	6.8	7.0	.986	1417	11.0	12.1	12.3	1.100
1563	6.9	6.9	7.1	1.000	1424	11.2	12.3	12.3	1.098
1597	7.2	7.5	7.6	1.042	(*)	11.2	12.8	13.0	1.143
1642	7.2	7.5	7.5	1.042	1425	12.4	14.5	14.5	1.169
1525	7.3	7.3	7.4	1.000	1420	12.7	14.3	14.6	1.126
1566	7.3	7.4	7.6	1.014	1428	14.4	17.0	17.3	1.181
(*)	7.3	7.4	7.6	1.014	(*♀)	15.0	16.1	16.5	1.073
1400	7.3	7.7	7.8	1.055	Av.	5.77	5.77	5.84	.982

TABLE 16.—*Correlation between the left and right chelæ and cephalo-thoracic length in first regeneration cases.*

[Data arranged in order of cephalo-thoracic length.]

Catalog No.	Cephalo-thoracic length.	Left chela-length.	Right chela, first regenera-tion.	Ratio of left chela to cephalo-thoracic length.	Catalog No.	Cephalo-thoracic length.	Left chela-length.	Right chela, first regenera-tion.	Ratio of left chela to cephalo-thoracic length.
1577	3.8	3.6	3.1	0.947	1564	4.7	4.5	3.7	.957
1580	3.9	3.7	3.1	.949	1732	4.8	4.6	3.8	.958
1624	4.2	3.7	3.8	.881	1536	4.9	4.7	3.9	.959
1516	4.2	3.8	2.9	.905	1596	4.9	4.8	4.0	.980
1545	4.2	4.0	(?)	.952	1592	5.0	4.5	4.4	.900
1581	4.3	3.9	2.6	.907	1530	5.0	4.6	4.0	.920
1578	4.3	4.0	3.0	.930	1606	5.0	4.9	3.9	.980
1589	4.4	4.1	2.7	.932	1540	5.0	5.1	3.8	1.020
1569	4.5	4.3	3.5	.956	1554	5.1	4.9	4.0	.961
1635	4.6	4.3	3.1	.935	1517	5.1	5.0	3.8	.980
1514	4.6	4.4	3.6	.957	1397	5.5	5.2	3.3	.945
1531	4.6	4.4	3.8	.957	1512	5.6	5.5	3.9	.982
1573	4.7	4.2	3.2	.894	1617	5.7	5.7	4.1	1.000
1633	4.7	4.4	3.8	.936	1612	5.7	5.8	(?)	1.018

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TABLE 16.—*Correlation between the left and right chelæ and cephalo-thoracic length in first regeneration cases*—Continued.

Catalog No.	Cephalo-thoracic length.	Left chela-length.	Right chela, first regenera-tion.	Ratio of left chela to cephalo-thoracic length.	Catalog No.	Cephalo-thoracic length.	Left chela-length.	Right chela, first regenera-tion.	Ratio of left chela to cephalo-thoracic length.
1535	5.8	5.8	4.4	1.000	1520	7.7	8.3	6.7	1.078
1733	5.8	5.8	4.0	1.000	1526	7.8	7.6	6.2	.974
1544	5.9	5.8	4.2	.983	1632	7.8	8.2	6.6	1.051
1521	6.1	6.1	(*)	1.000	1551	7.9	8.1	6.6	1.025
1562	6.1	6.3	5.2	1.033	1585	8.0	8.1	6.8	1.012
1603	6.2	6.0	4.9	.968	1642	8.0	8.4	(?)	1.050
1523	6.2	6.2	5.4	1.000	1607	8.3	8.3	7.3	1.000
1588	6.2	6.4	5.3	1.032	1597	8.3	8.8	7.6	1.060
1532	6.3	6.3	5.2	1.000	1593	8.4	8.8	6.9	1.048
1610	6.4	6.0	4.5	.937	1525	8.5	8.5	6.8	1.000
1541	6.4	6.3	5.5	.984	1400	8.6	8.8	(?)	1.023
1406	6.4	6.5	5.1	1.016	1561	8.8	9.1	8.3	1.034
1595	6.4	6.5	4.7	1.016	1412	9.0	9.5	6.0	1.056
1534	6.5	5.4	(?)	.831	1563	9.1	9.2	(?)	1.011
1605	6.5	6.2	4.6	.954	1419	9.1	9.3	8.3	1.022
1401	6.6	6.6	5.0	1.000	1422	9.1	9.4	8.2	1.033
1637	6.8	6.6	4.2	.971	1524	9.2	9.7	8.4	1.054
1634	6.9	6.4	5.2	.928	1414	10.0	9.6	7.2	.960
1568	6.9	6.8	5.6	.986	1636	10.0	10.5	(*)	1.050
1731	6.9	7.3	6.1	1.058	1409	10.2	10.6	8.6	1.039
1629	7.0	7.0	3.9	1.000	1423	11.0	11.4	9.4	1.036
1628	7.1	7.1	(?)	1.000	1528	11.0	11.8	9.5	1.073
1408	7.1	7.2	6.7	1.014	1416	11.3	11.8	(?)	1.044
1616	7.2	7.2	6.6	1.000	1421	11.6	11.2	10.3	.966
1591	7.3	7.5	6.5	1.027	1427	12.3	14.8	13.8	1.203
1405	7.4	7.4	6.1	1.000	1420	14.5	16.9	14.4	1.166
1410	7.4	7.6	7.2	1.027	Av.	6.81	6.85	----	.993

TABLE 17.—*Correlation between the left and right chelæ and cephalo-thoracic length in second regeneration cases.*

[Data arranged in order of cephalo-thoracic length.]

Catalog No.	Cephalo-thoracic length.	Left chela-length.	Right chela, second regenera-tion.	Ratio of left chela to cephalo-thoracic length.	Catalog No.	Cephalo-thoracic length.	Left chela-length.	Right chela, second regenera-tion.	Ratio of left chela to cephalo-thoracic length.
1394	4.0	3.9	3.0	0.975	1522	7.3	7.2	(*)	0.986
1577	4.2	4.3	(*)	1.024	1406	7.3	7.4	5.4	1.014
1594	4.4	4.1	3.1	.932	1627	7.3	7.7	6.4	1.055
1587	4.4	4.3	3.3	.977	1408	8.0	8.0	6.1	1.000
1580	4.4	4.4	3.8	1.000	1731	8.0	8.3	5.0	1.037
1575	4.5	4.4	3.6	.978	1616	8.1	8.5	7.0	1.049
1569	4.6	4.5	(*)	.978	1618	8.3	8.6	(*)	1.048
1398	4.7	4.5	3.3	.957	1591	8.3	8.7	6.9*	1.036
1545	4.8	4.5	3.0	.937	1529	8.6	9.3	7.3	1.081
1518	5.0	4.8	3.6	.960	1526	8.9	9.0	7.2	1.011
1633	5.3	5.2	(*)	.983	1411	9.7	10.1	7.7	1.041
1601	5.4	5.1	(*)	.944	1640	9.7	10.4	7.1	1.072
1514	5.4	5.2	3.7	.963	1419	9.9	10.7	8.9	1.081
1596	5.5	5.5	3.9	1.000	1415	9.9	10.9	(*)	1.101
1598	5.8	5.7	(*)	.983	1561	10.2	10.3	8.2	1.010
1554	5.9	6.1	4.4	1.034	1422	10.2	10.8	8.5	1.059
1402	6.0	5.9	(*)	.983	1524	10.2	10.9	8.9	1.069
1523	6.8	6.9	6.2	1.015	1413	10.4	10.9	8.8	1.048
1532	7.0	7.0	5.5	1.000	Av.	6.99	7.13	----	1.011
1610	7.1	7.1	5.5	1.000					

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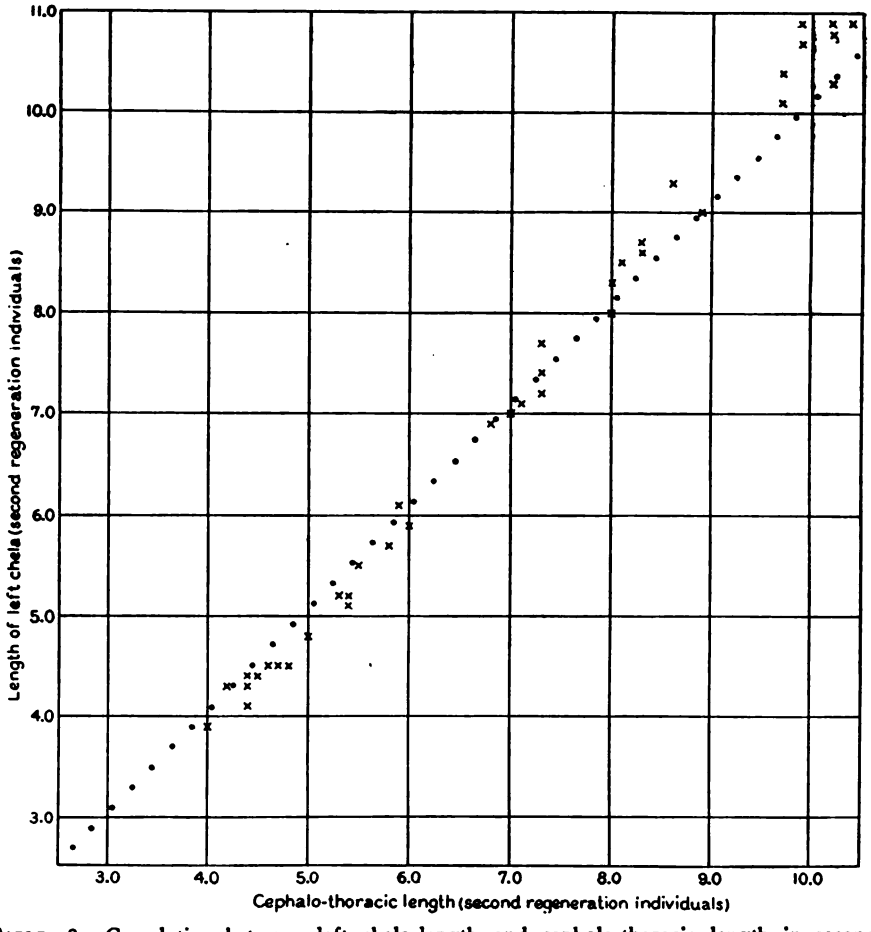

TABLE 18.—Correlation between left chela-length and cephalo-thoracic length in second regeneration cases. *Dotted line*, line along which all the data would be arranged if specific length of left chela were the same for all sizes of individuals.

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A tour of inspection in the Booby Colony. Illustrating the tameness of the birds.

Booby Colony looking West. The Yacht Physalia in the distance.

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V. A CONTRIBUTION TO THE LIFE-HISTORIES OF THE BOOBY (SULA LEUCOGASTRA) AND MAN-O'-WAR BIRD (FREGATA AQUILA).

BY FRANK M. CHAPMAN,
Of the American Museum of Natural History.

6 plates.

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A CONTRIBUTION TO THE LIFE-HISTORIES OF THE BOOBY (SULA LEUCOGASTRA) AND MAN-O'-WAR BIRD (FREGATA AQUILA).

By Frank M. Chapman.

INTRODUCTORY.

The expedition on which the observations herein recorded were made was undertaken primarily to secure specimens, accessories, photographs, and data to be used in the preparation of a "habitat group" of the booby and man-o'war bird in the American Museum of Natural History. Dr. Alfred G. Mayer, in command, George Shiras, 3d, and the writer, sailed from Nassau, March 31, 1907, aboard the *Physalia,* for Cay Verde, about 230 miles to the southeast, where the birds desired were reported to nest. Unfavorable weather prolonged our voyage to the cay to nine days, and this delay, in connection with continued unpleasant weather and the absence of a harbor, made it undesirable to remain at the cay longer than was necessary for the accomplishment of our object. While, therefore, the trip was successful so far as collections for groups were concerned, the three days and nights (April 9 to 11) passed on the cay permitted us to make only the most casual study of the habits of the birds found nesting there. Nevertheless, with the coöperation of Dr. Mayer and Mr. Shiras, information was gathered which appears to deserve record as a contribution to our knowledge of Bahaman bird-life, and particularly to the biographies of the man-o'-war bird and booby, about the nesting habits of which, in this region, little appears to have been written.

CAY VERDE.

Cay Verde lies on the eastern edge of the Columbus Bank, 30 miles southeast of Little Ragged Island. It is about 0.5 mile long by 0.25 mile in greatest width, the longer axis lying approximately north and south, and, roughly estimated, contains some 40 acres. On the west and south, or shallow, Bank sides there are steeply shelving beaches, where, under favorable conditions, a landing may be easily made; on the eastern side the deep-blue waters of the ocean break directly against the characteristic, water-worn limestone rock, of which Cay Verde, in common with other Bahama islands, is composed. At the northern end, where the islet terminates in a point, this rock is but little above sea-level. Southward it gradually increases in

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height and, with pronounced irregularities in coast line, reaches a bluff-like elevation of 75 feet at the southeastern extremity of the islet.

About one-eighth of the surface of the island is covered with a dense growth, chiefly of sea-grape (*Coccolobis uvifera*), but with a liberal mixture, mainly about the borders, of a "prickly-pear" cactus (*Opuntia*) and sea-lavender (*Tournefortia gnaphalodes*). Where sufficient soil has accumulated, the remainder of the island supports a growth of coarse grasses, sparse on the higher and rockier portions, more luxuriant in the lower portions, particularly about the margins of a small salt pond, the size of which was dependent upon conditions of tide and wind. There is no fresh water on the cay.

BIRD-LIFE.

In the literature of ornithology, Cay Verde figures only in Bryant's "List of Birds seen at the Bahamas from January 20 to May 14, 1859," where it is casually mentioned[1] as a breeding-place of the tropic-bird (*Phaëthon flavirostris*). This author writes at some length of the nesting habits of the booby and man-o'-war bird as observed on San Domingo Cay and the Ragged Islands, respectively, but does not refer to the colonies of these birds on Cay Verde. Possibly he did not himself visit Cay Verde, where doubtless both the species of birds named have nested for a prolonged period; this cay, so we were informed, having, some ten years ago, been the site of a guano industry, which flourished until all the available deposit had been removed.

The writer's information in regard to the birds of Cay Verde was obtained from the late D. P. Ingraham, who, as a collecting naturalist, visited the cay about 1891. Mr. Ingraham's information in regard to the presence of boobies and man-o'-war birds was fully verified. In May (he also wrote) great numbers of terns (doubtless *Sterna fuliginosa, S. anæthetus,* and *Anous stolidus*) and a few tropic-birds come to the cay to nest.

No land birds appear to be resident on Cay Verde, but it is evidently visited by numbers of migrants. During our stay the following species were noted:

Common name.	Scientific name.
Audubon's shearwater	Puffinus l'herminieri
Sooty tern	Sterna fuliginosa
Great blue heron	Ardea herodias
Little blue heron	Florida cærulea
Black-necked stilt	Himantopus mexicanus
Greater yellow-leg	Totanus melanolucus
Little yellow-leg	Totanus flavipes
Least sandpiper	Tringa minutilla
Turnstone	Arenaria morinella
Osprey	Pandion haliætus

[1] Proc. Bost. Soc. Nat. Hist., VII, 1859, p. 102.

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Common name.	Scientific name.
Duck-hawk	Falco peregrinus anatum
Kingfisher	Ceryle alcyon
Mangrove cuckoo	Coccyzus minor maynardi
Gray kingbird	Tyrannus dominicensis
Savanna sparrow	Passerculus sandwichensis savanna
Palm warbler	Dendroica palmarum palmarum
Myrtle warbler	Dendroica coronata
Yellow-throat	Geothlypis trichas

Audubon's shearwater was doubtless breeding on the cay in some of the innumerable holes in the limestone. No attempt was made to discover it, but the abundance of the birds from nightfall until midnight, as betrayed by their singular calls, together with the absence of other land nearer than 30 miles, leaves little doubt of their presence on the cay. The birds should have been laying at this time, if one may judge from observations made by the writer in May, 1902, in the Washerwoman Keys, off Andros.

A single sooty tern was seen late one afternoon, and numbers of these birds, with probably also bridled terns, were heard flying about the cay after nightfall. Possibly they may have roosted on the cay, or their visit may have had some connection with their later occupation of it as a nesting-ground.

Three duck-hawks living on the cay apparently found sufficient subsistence in the shore-birds (*Limicolæ*) which visited it, and of which they were several times seen in pursuit.

The presence of the birds above mentioned indicates that Cay Verde would be an admirable station for the study of the migration of birds throughout this region. The small size of the cay would permit the taking of fairly accurate daily censuses, while the distance from the nearest land makes it the only available stopping-place in a large area. It is to this isolation that the presence of large numbers of breeding birds on the cay may be chiefly attributed. Animal food is always at a premium in the Bahamas, where indigenous mammalia are virtually absent, and conditions are generally not favorable for the support of domesticated varieties.

The Bahaman negro considers all flesh edible, and those bird rookeries which were most accessible have long ago been devastated for food. The colony containing thousands of man-o'-war birds, which Dr. Bryant (*l. c.*) found on Ragged Island, no longer exists; its extinction, doubtless, being due to the habit, of which we were told, of collecting young man-o'-war birds, salting them, and shipping them as food to other islands.

THE BOOBY.

HABITS.

Although, as a tropicopolitan species, the booby (*Sula leucogastra*) is found throughout the West Indies northward, at least to the mouth of the St. John's River, Florida (where on March 11, 1907, the writer saw 12

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individuals), Bryant, as has been before remarked, appears to be the only naturalist who has recorded an authentic description of its nesting in this region. The booby's claim to breeding within the limits of the United States rests on Audubon's account[1] of its nesting on "Noddy Island" in the Tortugas, where, in May, he found that "most of the birds were sitting" on "large and flat" nests "formed of a few dry sticks, covered and matted with sea-weeds in great quantity" and placed "on the top of a bush," while the down-covered nestling is said to have had "the bill and feet of a deep, livid blue or indigo color." But other writers are agreed that *Sula leucogastra* begins to nest in this region in February, lays usually two eggs (always on the ground), uses little if any nesting material, and the bill and feet of the nestling are yellowish-green.

Bryant (*l. c.*), who has commented on this discrepancy, thinks that Audubon may have mistaken nests of the brown pelican for those of the booby; but Audubon's familiarity with the pelican's nesting habits, together with his statement that in all the "booby's" nests examined only one egg was found, some of which had the "chick nearly ready for exclusion," renders Bryant's hypothesis improbable. Furthermore, Audubon's detailed statement that there was a "constant succession of birds coming in from the sea with food for their young, consisting chiefly of flying-fish and mullets, which they disgorged in a half-macerated state into the open throats of their offspring," shows, in spite of some looseness in the description of the manner of feeding, that he had abundant opportunity to observe the parents at close range. That his bird was not *Sula leucogastra* there can be small room for doubt, but it is by no means so certain that it was not the red-footed booby (*Sula piscator*), a species which has been found nesting in Cayman Brac, South of Cuba,[2] and which nests in bushes and lays but one egg.

It is true that Audubon both describes and figures *Sula leucogastra;* nevertheless he observes "that none of the birds which were still brown had nests, and that they roosted apart, particularly on Booby Island (a sand-bar), about 8 miles to the northeast of the Tortugas Lighthouse," which he had found to be "covered with boobies."

This view of the case finds support in the fact that the collection of the Philadelphia Academy of Natural Sciences contains a specimen of *Sula piscator* collected by Audubon in Florida and labeled by him "*Sula fusca,*" under which name *Sula leucogastra* was known to him. It is evident, therefore, that Audubon confused the two species, an error which may account for his figuring and describing *Sula leucogastra* when writing of the nesting habits of what appears to have been *Sula piscator.*

[1] Orn. Biog., III, pp. 63–77.
[2] Maynard, Cont. to Science, I, pp. 40–48, 51–57.

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Camp on Cay Verde.

Man-o'-War Birds over nests in sea grapes.

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Fig. 1. Female Man-o'-War Bird alighting.

Fig. 2. Female Man-o'-War Bird leaving nest.

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THE CAY VERDE COLONY.

A partial census of eggs and young led to the conclusion that there were about 1,500 pairs of boobies nesting on Cay Verde. They were distributed in several groups, where the comparatively level surface and sandy soil furnished favorable nesting conditions. In most instances the young were covered with down, with the brown second plumage more or less evident in wings and tail. A few birds of the year were already a-wing and several nests contained fresh eggs. For the greater number of birds, however, the nesting season, as Bryant has stated, evidently begins in February.

THE ADULT BIRDS.

One or both of the adults remain, as a rule, with the young. On March 9, the birds awoke at 5^h 15^m a. m., when for the ensuing 10 or 15 minutes there was a subdued kind of quacking, and some birds were seen flying. At 5^h 30^m several hundred birds left the rookery in a body to go a-fishing, this being the first general movement. Individuals returned at intervals during the day and evidently changed places with the bird left at the nest, which in turn went out to feed and to gather fish for the young. There was no concerted return movement until dusk, when flocks of birds came in from the sea, the last-comers not arriving until after dark. In the meantime the man-o'-war birds had retired, and it is not impossible that the boobies have acquired the habit of "staying out late" to avoid being robbed of their food by the man-o'-war birds, which at times attacked them as they approached the cay and forced them to disgorge.

Sitting or brooding birds spend the night upon the nest with the mates standing at their sides, but the close resemblance of the sexes rendered it impossible to distinguish them at this time. When the young is too large to be brooded, it passes the night on the ground between the two parents, which stand on either side, all three with their heads tucked under their scapulars.

When perched on rocks about the border of the island, boobies showed a decided fear of man and generally flew before one had approached to within 30 yards of them; but when on their nests they were conspicuously tame, the degree of tameness being related to the advance of the nesting season. A bird with newly hatched young would not, as a rule, leave the nest unless actually forced to do so, and it would strike so viciously at anyone approaching that it was well not to venture within its reach. This was the extreme development of parental instinct, which now gradually diminished as the young increased in size. Evidently as a result of excitement caused by our presence, the birds which remained to defend their young threatened us with their bills, picked up bits of sticks or grasses only to drop them and pick them up again, and even struck at their own young in a confused and aimless manner. The young also had this habit. The report of a gun occasioned but little alarm among the boobies, some of which, with their young near my feet, did not fly when the gun was discharged.

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In spite of the apparent sociability expressed by their communal habits, the boobies immediately resented trespass on their home site by one of their own kind. Where the nature of the ground permitted, their nests were placed with more or less regularity 6 to 8 feet from one another. As long as a bird remained within its own domain, having a diameter of approximately 6 to 8 feet, it was not molested; but let it or its young advance beyond these limits and they were promptly attacked.

So closely, however, are the birds confined to their own little areas that difficulties of this kind are rare, and under normal conditions peace reigns in the rookery. But when, as we walked through the rookery, the birds in escaping from the larger evil forgot the lesser one and inadvertently backed on to a neighbor's territory, the unusual cause of the trespass was not accepted as an excuse and they found the " frying-pan " worse than the " fire," as the enraged owner, with bristling feathers, furiously assailed them with open bill, sometimes taking hold. At these times, and whenever the birds were alarmed, they gave utterance to hoarse, raucous screams or screeches, though as a rule they were comparatively silent.

THE NEST.

The booby's nests on Cay Verde were usually slight hollows in the ground, with often a scanty lining or rim of dried grasses, but in some instances even this humble preparation for housekeeping was lacking, and the eggs were laid without pretence of nest.

EGGS AND YOUNG.

About 98 per cent of the boobies nesting on Cay Verde had young, some of which were newly hatched, while a few were on the wing, but the largest number were beginning to acquire flight feathers. Of the nests, 35 contained eggs, of which 21 held 2 eggs, while in 14 there was but 1; but possibly in some, if not most of these, another egg would have been laid. As a rule, therefore, there were 2 eggs, this confirming previously recorded observations on the nesting habits of this species. On the other hand, 2 young were the exception. Of 740 nests counted by Dr. Mayer on the east side of the cay, only 2 contained young, and both pairs were well grown and approximately the same size.

Examination of the eggs contained in sets of two showed that either there was a marked difference in the development of the embryos or that one or both eggs were infertile. For example, of 13 nests containing 2 eggs, in 3 nests both were bad; in 10 both were good, but with every good pair there was about a week's difference in the age of the embryo. In 6 nests each containing one young and one egg, 5 of the eggs were decomposed.

With those boobies which lay 2 eggs, apparently a week intervenes between the laying of the first and second egg, and to this unusual irregularity,

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in connection with the high percentage of infertility, we attribute the discrepancy between the number of eggs laid and the number of young reared.

Our studies were not sufficiently prolonged to enable us to determine whether, when both eggs were fertile, the young first hatched survived or whether, through continued incubation of the remaining egg, it starved and the young hatched from the last-laid egg lived; but in one instance a nest was observed containing a lately hatched dead young and an egg with an embryo.

The case is unique among birds, as far as I am aware, but that the data on Cay Verde do not reveal an exceptional condition is apparently proven by the observations of Walter K. Fisher[1] in the Leeward Islands of the Hawaiian group, where both *Sula cyanops* and *S. leucogastra* were found to lay 2 eggs and rear but 1 young.

The young booby is born practically naked, and since exposure to the sun before the downy plumage is developed would result fatally, it is constantly brooded, one parent immediately replacing the other when the brooding bird is relieved. Brooding continues even when the white down is well developed and the young bird, then too large to be wholly covered by the parent, lies flat on the ground, the head exposed, the eyes closed, apparently dead. This relaxed attitude is also taken by young which are not sheltered by the parent, and we were not a little surprised on several occasions, when about to examine an evidently dead bird, to have it jump up and with a trumpeting call blare at us with open mouth. Nor do they rely only on the voice for defense, but use the bill effectively, and, as has been remarked, they possess with the adult the somewhat ludicrous habit of venting their feelings by picking up bits of stick and grass.

Compared with other rookeries I have visited, the mortality among young boobies on Cay Verde—aside from the prenatal mortality already referred to—was surprisingly small. This I attribute to the isolation of the cay, which permits the birds to rear their young with little or no intrusion by man, whose presence, even as a visitor, results in great confusion and consequent death among the young of ground-nesting colonial birds.

The young were fed on squids and fishes, which in a more or less digested condition they obtained by thrusting their heads and necks down the parent's throat, a manner of feeding common to all the Steganopodes with whose habits I am familiar (including *Pelecanus, Fregata, Phalacrocorax,* and *Anhinga*). I have not, however, seen *Phaëthon* feeding its young, and it would be interesting to know whether this tern-like member of the order has a similar method of administering food.

Evidently but one brood is reared, since approximately 3 months must elapse after the egg is laid before the young can fly and care for itself.

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[1] Birds of Laysan and the Leeward Islands, Hawaiian Group, U. S. Fish Comm. Bull., 1903, pp. 28–30.

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DEVELOPMENT OF PLUMAGE.

At birth the young booby seems to be featherless, but closer examination shows that the white natal down is appearing on all the dorsal pterylæ and upon the posterior margin of the wings, including the alula. The abdominal pterylæ show as yet no evidences of feather growth. The down plumage grows rapidly and, when developed, almost entirely covers the chick's body—the gular pouch, orbital and loral regions, and inner margin of the humerus being the only apteriæ.

The second, juvenile,[1] or nestling plumage of which the down is merely the apical portion,[2] follows the down by continuous growth, the down being a white filamentous fringe to the stronger, brownish feather of the second plumage. This plumage may be first seen in the *pterylæ alaris,* the primaries appearing first, to be quickly followed by the secondaries, tertiaries, and feathers of the alula. At almost the same time the rectrices become evident: soon after the uropygial feathers come. Greater, median, and less upper wing-coverts and tail-coverts emerge, before feathers of the second plumage appear upon the body proper, except those growing from the *pteryla uropygii.*

In the next oldest specimen the juvenile plumage of the breast and abdomen approaches full development and was evidently the first to grow upon the body tracts, except as noted above. On the back the juvenal plumage, although well grown on the *pteryla humeralis,* is but just appearing on the anterior portion of the *pteryla spinalis,* although posteriorly the feathers are larger. The crural and femoral tracts, the outer margins of the manus, a strip at the base of the secondaries, and the whole head and neck are still clad in down.

In the succeeding specimen, the second or juvenal plumage is essentially complete, except upon the foreneck, where it is just emerging. This bird is almost uniform grayish-brown above; the upper tail-coverts are slightly browner; the exposed portion of the remiges and rectrices show a somewhat frosted effect; the primaries are decidedly blackish; the lower breast and abdomen are grayer than the dorsal plumage; the upper breast (with which the throat feathers would apparently agree) is decidedly browner. This is the flight plumage. When it gives way to the succeeding plumage does not appear to be known.

MAN-O'-WAR BIRD.

Descriptions of the nesting habits of the man-o'-war bird (*Fregata aquila*) are based chiefly on studies made in the Pacific. Bryant,[3] whose description of the nesting habits of the booby has already been cited, gives us apparently the only account of the breeding of this species as it occurs in

[1] Dwight, Annals N. Y. Acad. Sci., XIII, pp. 73–360.
[2] Jones, Lab. Bull., No. 13, Oberlin College, pp. 1–18.
[3] Proc. Bost. Soc. Nat. Hist., VII, 1859, p. 126.

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Booby, Nest, and two Eggs.

Pair of Boobies with young in which remiges and rectices are appearing.

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Fig. 1.

Fig. 2.

Fig. 3.

Fig. 1. Boobies.
Fig. 2. Female Man-o'-War Bird and young.
Fig. 3. Showing habit of picking up sticks, etc., when excited.

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West Indian waters, though it of course has many nesting resorts in this region. Gundlach's[1] notes on the bird in Cuba appear to be based on Audubon's observations. Audubon writes[2] that he found the man-o'-war bird breeding in the Florida Keys "about the middle of May" and even describes its manner of collecting nest-building material; but it is difficult to make his account agree with the known habits of the species. It is true that in May the man-o'-war bird appears in large numbers on the Florida Keys, but such flocks contain young of the year and their presence is due to post-breeding wandering. Audubon states that the man-o'-war bird lays 2 or 3 eggs, "more frequently the latter number," whereas there is abundant testimony to prove that the usual number is 1. Furthermore, the young are covered with snowy white, not "yellowish white" down, as Audubon writes.

Equally important with these errors of commission is Audubon's failure to mention the man-o'-war bird's remarkable habit of inflating its gular pouch to the size of a toy balloon. This is far too conspicuous a feature of the mating and early nesting season[3] to have escaped notice and mention.

What the nests were that Audubon mistook for those of *Fregata aquila* I do not pretend to say; but it is reasonably certain that his identification of them was incorrect.

THE CAY VERDE COLONY.

The luxuriant growth of cactus among the sea-grapes in which the man-o'-war birds nested added to the difficulty with which these thickly branched, shrubby trees were penetrated, and we did not attempt to make a census of the number of birds of this species which were breeding on Cay Verde. We estimated, however, that there were between 200 and 300 pairs.

The nesting season seemed to be about as far advanced as it was with the booby, most of the nests containing half-grown young, but some held fresh eggs, while a few birds of the year were already on the wing. Their manner of nesting prevented us from studying the nesting habits of the man-o'-war bird with the ease which attended our observations of the boobies; and I have but little to record concerning the biography of this species. The specimens collected, however, present some interesting facts (apparently not recorded hitherto) in regard to the development of plumage in the man-o'-war bird.

THE ADULT BIRDS.

The man-o'-war birds awoke at about the same time as the boobies, and at 5^h 30^m a. m. were sailing over their rookery. From this time until they

[1] Journ. für Orn., 1857, p. 239.

[2] Orn. Biog., III, p. 495.

[3] See W. K. Fisher, Birds of Laysan and the Leeward Islands, Hawaiian Group, U. S. Fish Comm. Bull., 1903, p. 30, pl. VIII, figs. 39, 40.

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retired, considerably before the boobies, and while it was yet light, a flock of birds was constantly over the sea-grapes. The birds may be said to have perched in the air above their homes. Only one bird is in attendance on the young at the same time. Both sexes assumed this duty, as well as the task of incubation: but there appeared to be no regularity as to when male or female should be on guard.

The man-o'-war birds were less tame than the boobies and, as a rule, left the nest when one approached to within 30 or 40 feet of them. When, however, they were brooding newly hatched chicks they showed more bravery.

In most instances the gular pouch had faded from carmine to orange, and only one individual was seen with the pouch inflated, as Fisher has described it (*l. c.*). As I attempted to approach this bird, the pouch was suddenly deflated.

The man-o'-war birds were not seen to devour the young of their own species, as they have been said to do; nor were they observed to capture young boobies. Occasionally they chased the adult boobies and made them disgorge in the air, but evidently, in the main, they did their own purveying, flying-fish being taken from the throat of one bird that was shot.

The adults were not heard to utter a sound.

THE NEST.

The nests are frail, open-worked, slightly hollowed platforms, composed of small sticks and twigs, placed in the tops of the sea-grapes, at a height of 6 or 7 feet, or among the cactuses within 2 feet of the ground. Several nests are often placed in one bush within reaching distance of one another. They become matted with filth as the young increase in size. One adult was seen carrying nest-building material in its bill.

THE EGG AND YOUNG.

The man-o'-war bird lays but one egg, and in a number of nests fresh eggs were found. The young are born naked and are brooded by the parents. As they increase in size and become covered with white down, their wings seem to be much too large for them to hold close to the body, and relaxing, are permitted to rest on the nest. Their whole attitude suggests extreme dejection; not only do the wings droop, but the head often hangs over the edge of the nest. When approached they utter a squealing, chippering call, and snap their bills with a rattling sound, both the note and action strongly suggesting similar habits of the young brown pelican.

THE DEVELOPMENT OF PLUMAGE.

The newly hatched man-o'-war bird is without down, except upon the tail, alula, and those portions of the forearm from which the remiges grow. When fully developed, this natal down, while not so uniformly

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dense as in *Sula leucogastra,* grows from all parts of the body except the inner surface of the legs, the gular pouch, and the throat. On the interscapular region, however, the natal down is not given much opportunity for growth, the black feathers of the second or juvenile plumage appearing in the *pteryla humeralis* and *pteryla dorsalis* immediately after the down of these tracts has pushed through the skin, if indeed—in some cases—they do not emerge without being preceded by down. The development of these interscapular feathers is remarkable, and before there is any evidence of the remiges and rectrices they cover the back like a mantle, as may be seen in the photographs of young birds in the nest.

It is surprising that in a bird famed for its power in flight, and possessed of exceptional length of wing and tail, the feathers of these parts, contrary to the general rule, should not take the lead in development. Comparison of the young of *Fregata* and of *Sula leucogastra,* for example, in which wing-feathers of the second plumage are just evident, shows that while the former has the whole interscapular region black, some of the feathers being 3.75 inches in length, *Sula* shows as yet no signs of second plumage in this region.

Not only are the wing feathers in *Fregata* late in appearing, but the secondaries precede the primaries, the former averaging 2 inches in length, with the greater and median coverts showing, when the latter are just observable. At this time the feathers of the uropygium and tail become evident; the outer tail feathers appear considerably in advance of the others, and give us a hint of their subsequent extreme length; but the order of growth of the feathers of the wing does not suggest that exceptional development of the feathers of this member which so distinguishes *Fregata.*

Specimens are lacking in which to trace the development of the plumage in detail. The largest bird in the series shows, however, further departure from the usual order in feather growth in the young bird, by having the second plumage of the head appear while the rectrices and remiges are still small and the natal down still remains on the lower back, the crural and femoral tracts, a large part of the ventral tracts, and at the base of the secondary and primary wing-coverts.

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Fig. 1.

Fig. 2.

Fig. 1. Young Man-o'-War Birds. Showing great development of the inter-scapulars and relaxed wings.

Fig. 2. Twin Boobies.

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VI. THE HABITS AND EARLY DEVELOPMENT OF LINERGES MERCURIUS.

BY EDWIN G. CONKLIN,
Professor of Zoology, University of Pennsylvania.

8 plates, 2 text figures.

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THE HABITS AND EARLY DEVELOPMENT OF LINERGES MERCURIUS.

By Edwin G. Conklin.

During a part of April and May, 1905, while a guest of the Carnegie Institution of Washington at its Marine Laboratory at Tortugas, Florida, I had opportunity to study the habits and early development of the scyphomedusan *Linerges mercurius* Haeckel, but was unable at that time to complete the work, owing to the sudden disappearance of these jelly-fishes. I spent the month of July of the same year at the Bermuda Biological Station, but did not find a single specimen of these medusæ until the day on which I sailed for home, when they appeared in great numbers, but too late for me to continue my work upon them. During the month of April, 1907, I was again the guest of the Carnegie Institution at its temporary station at Nassau, New Providence, Bahamas, and there obtained enough of these jelly-fishes to continue the work which had been begun two years before. But here also the work was interrupted by the sudden disappearance of these animals; however, I have decided to publish this report of my work, although it is still in many respects incomplete, since I may not again in the near future have an opportunity to study these forms.

HABITS.

Occurrence.—The sudden appearance, in great numbers, of *Linerges* and its equally sudden disappearance has been noted by other observers. The animals began to appear when I first arrived in Tortugas, April 24, and increased in numbers until April 28, on which day they were present in countless myriads, usually stretching in great windrows across the surface of the water. On April 29 very few could be found; on April 30 an extended search all around the fort and harbor failed to reveal more than 20 individuals; on subsequent days none were present. They appeared and disappeared in a similarly sudden manner at Nassau, between April 23 and April 30, and at Bermuda between July 27 and August 1.

How is this sudden appearance of the *Linerges* swarm to be explained? There is no evidence that they drift in on ocean currents from some other locality and disappear in the manner in which they came. On the contrary, they frequently occur in relatively inclosed areas, where currents are not strong, and before or after the swarming they are not to be found in the

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surrounding waters. On the other hand, I have observed that when they first appear they come up from deep water, and their disappearance can be seen to be due to their sinking from the surface into greater depths. In 1907 I first found them outside of Nassau harbor far below the surface; day after day they were found nearer the surface, until the great swarm appeared, after which they again settled into deeper water.

The cause of their sudden disappearance may be observed in the laboratory as well as in nature. The sexual products are shed during the swarming and after the gonads are emptied the medusæ settle to the bottom and soon thereafter begin to disintegrate, as may readily be seen in an aquarium. It can also be observed that the same thing takes place in nature, where many dead or dying medusæ may be found over the bottom in shallow water after the swarm has disappeared. The enormous numbers of the swarm and its limited duration, as well as the fact that the medusæ come up from deep water, all indicate that they must be formed and set free in the immediate vicinity of the place where they appear at the surface.

Movement to the surface is an active and not a passive process; the medusæ and their eggs are heavier than water, and they settle to the bottom when undisturbed or when movement ceases. The movements to or from the surface are not correlated with the intensity of light, as is the case in so many pelagic organisms, for during the swarming these medusæ are at the surface at all hours of the day and, so far as I could observe, of the night also. Furthermore, they appear at the surface at no other time than the swarming period. It is highly probable that the movement to the surface is correlated with the ripening of the sexual products; and it is certain that the swarming is of importance to the species, since the ripe males and females are thus brought near together at the time when the sex products are ready to be shed. The collection of these medusæ into windrows is of great advantage in insuring the fertilization of the eggs, but it is probably not brought about by the activities of the animals, other than those which serve to keep them at the surface of the water. Probably the winds and waves gather them into the windrows.

Movements.—The normal movements of *Linerges* are of two kinds: (1) the pulsations which drive the animal forward in swimming, and (2) rhythmical flattening of the bell, by bringing together opposite sides, so that the opening into the bell is elongated first in one direction, then in another. These latter movements are especially prominent when the medusæ are confined within a small space, are much irritated, or when lying on the bottom. This flattening of the bell may be violent, in which case the opening into the bell becomes slit-like, or it may be weak, in which case the bell opening is quadrangular or triangular in shape. When violent, the directions of flattening are alternately almost at right angles, but not quite. When viewed

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from the oral pole the successive axes of elongation (or flattening), in some cases at least, pass slowly around the bell in an anti-clockwise direction.

In the normal forward movements the animal always rotates in an anti-clockwise direction, when viewed from the oral pole. They may stand for some time with the aboral pole at the surface of the water and rotate rapidly in the direction named, without much forward movement, but always with pulsations of the bell. The cause of this rotation lies in the lobes or lappets at the margin of the bell, which is so arranged that the right side of each lappet (when viewed from the center of the oral pole) lies nearer the oral surface of the bell than the left side, and usually the right side overlaps the left side of the next lappet to the right. Therefore, in pulsations of the bell, water is directed out in a clockwise spiral, which causes the animal to rotate in an anti-clockwise direction. If the lappets are cut off, the bell may continue to pulsate, but the animal only moves forward slowly and does not rotate. If a hole is cut in the aboral side of the bell and the stomach and manubrium removed, the bell continues to pulsate and the animal moves forward normally and with anti-clockwise rotation, though these movements are slower than normal. If the whole margin of the bell is cut off it continues to contract for a long time, the movements being almost entirely such as flatten the ring alternately in one direction and then in another (second type of movement described above). The remainder of the bell, after the margin has been removed, is usually quiescent, but may sometimes contract slowly. If the marginal ring is cut in two so as to form a long, narrow ribbon, it still continues to contract rhythmically for several hours.

Egg-laying.—The males and females of this species may be distinguished by the color of the ripe gonads; the male gonads are brown, those of the female slate or blue-gray.

The eggs are laid and fertilized about 8 a. m., and at no other period of the day. The egg-laying begins by the escape of a few isolated eggs from a few individuals, but in a short time a perfect "epidemic" of egg-laying takes place, after which no other eggs are laid until the following day. The eggs escape in masses held together by a thin jelly. Occasionally small, immature eggs are laid along with the mature ones, but this is rare; usually all the eggs are mature when laid. Each egg is closely surrounded by a very thin transparent membrane which persists until the gastrula stage. Outside this membrane are numerous small, brown bodies which are probably follicle cells.

The spermatozoa are shed at the same time that the eggs are laid, but I was unable to determine whether one of these processes stands in a causal relation to the other.

The egg-laying usually takes place very close to the surface of the water, after which the eggs gradually settle through the water to the bottom of the aquarium. If the gonads have not been emptied on the first day the medusæ

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may survive and shed their sex cells on a subsequent day. When the gonads have been emptied the medusæ settle to the bottom and die.

DEVELOPMENT.

The egg-structure.—The newly-laid eggs vary somewhat in size, but average about 240 μ in diameter. They are blue or blue-gray in color. They show no polar differentiation save that the germinal vesicle is frequently (perhaps always) eccentric toward the future maturation pole.

The living eggs are too opaque to show much of their structure, and eggs which have been fixed and sectioned often show certain artifacts, the results of the reagents used. It is therefore difficult to determine with certainty what the normal structure of the egg is. In the living egg, as well as in material fixed in various standard fluids there is a peripheral layer of clear protoplasm in which there are few yolk spherules, and these quite small; this peripheral layer may therefore be considered a normal feature. In the most perfectly fixed material there is a layer of densely packed yolk spherules just inside the peripheral layer; while within this is a central area containing fewer yolk spherules scattered through a fluid or semi-fluid matrix which probably represents dissolved yolk (figs. 37, 39). In material fixed in picro-acetic or picro-sulphuric acid the peripheral layer may be separated by a space from the deeper-lying parts of the egg; on the other hand, in material fixed in Hermann's or Flemming's solutions such a space does not appear, and it is evidently an artifact. Furthermore, in picric fixation the central area is more homogeneous in appearance and the yolk is more compact than in material fixed in Hermann's or Flemming's fluids. It is difficult to decide which of these fixations represents more nearly the normal condition of the central area, but this is not a matter of much importance, since in all the fixations used the yolk spherules are less densely crowded together in the central area than in the surrounding layer.

Hargitt (1906) found a concentric arrangement of the cytoplasm of the eggs of *Pennaria,* after they had been fixed in picro-sulphuric solutions, but he regards this as an artifact, due to poor fixation. However, so far as the peripheral layer of protoplasm is concerned, it has been seen in the living eggs of many cœlenterates; it is therefore not an artifact, nor is it of rare occurrence. As to the central area of the egg, it is known from a study of the living transparent eggs of several genera of medusæ and ctenophores that the substance of this area is frequently of a foamy, or vacuolar, character and that it contains only a scanty reticulum of protoplasm and but few yolk spherules. I conclude, therefore, that both the peripheral layer and the central area shown in my sections of the *Linerges* egg are of normal occurrence. The layer of closely packed yolk spherules, which surrounds the central area, is the only layer which has not been observed either in *Linerges* or elsewhere in the living egg, but if both peripheral and central areas are faith-

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fully fixed in my sections of the *Linerges* egg it seems probable that the layer between these two is also a normal feature of this egg.

Furthermore, by means of high centrifugal force the substances of the egg of *Linerges* may be separated into three distinct zones, the lightest of which is clear protoplasm, the heaviest a yellow substance crowded with yolk spherules, and intermediate between these a zone of blue or blue-gray material. It is difficult to determine whether these zones correspond to the three concentric layers just described, but they at least show the presence of substances of different specific weights in the unsegmented egg.

There are two kinds of spherules within the oöplasm; (1) large yolk spherules ranging from 3 to 9 μ in diameter, and (2) small spherules, densely black after Flemming's fluid, which are from 0.5 to 1 μ in diameter. The latter are at first distributed quite uniformly throughout the oöplasm, but during mitosis they gather closely around the spindles and nuclei.

The germinal vesicle is relatively large and contains a single large nucleolus which is usually vacuolated and in some cases an additional smaller nucleolus may be present (plate 1, figs. 1, 2). The chromatin consists of small granules scattered through the achromatic ground substance (plate 1, fig. 1). In the prophase of the first maturation this chromatin is differentiated into oxychromatin granules and into a relatively small number of basichromatin rods (plate 1, fig. 2), which in certain stages have the form of tetrads.

Maturation and fertilization.—As maturation approaches, the germinal vesicle moves up to the periphery of the egg; in fact, the outer side of the vesicle comes into contact with the cell membrane and in some cases (probably abnormal) the germinal vesicle is protruded from the egg as if it were being squeezed out bodily (plate 1, figs. 1, 2). When the wall of the germinal vesicle dissolves a relatively enormous quantity of achromatic substance escapes into the cell body.

Two polar bodies are formed in the usual manner; however, both first and second maturation spindles are very small, about 0.002 part of the volume of the germinal vesicle, and they exhibit neither centrosomes nor polar rays. During the formation of the first polar body a lobe of clear protoplasm appears at the vegetal pole, just as is the case among annelids and mollusks. This lobe soon disappears and does not again reappear at the second maturation division or the first cleavage, as it does in the cases of annelids and mollusks (fig. 3). In one or two instances I have seen the head of the spermatozoon within or just central to this lobe (fig. 4), and it is possible that the lobe is formed at the point of entrance of the sperm. If this be true the sperm enters at or near the vegetal pole, as is the case with so many animals.

Hargitt (1906) believes that in *Clava, Pennaria,* and *Eudendrium* no mitotic figures are present during maturation and "that the reduction phenomena of maturation may well be accomplished without any of the

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complex and spectacular processes of mitosis." No confirmation of such a view can be found in the egg of *Linerges*, where both maturation spindles may be seen in eggs stained and mounted entire, as well as in sections.

First cleavage.—The egg nucleus remains near the maturation pole and the sperm nucleus migrates up through the egg until it comes to lie just beneath or alongside of the egg nucleus (figs. 5, 39). The cleavage amphiaster then arises, but I have not observed the details of its origin. The chromosomes are then divided in the usual manner and the daughter nuclei are formed by the fusion of chromosomal vesicles (fig. 6). In the telophase of the division each of the daughter nuclei is sometimes composed of two equal vesicles (fig. 7) which probably represent the halves of the egg and sperm nuclei, the gonomeres of Haecker (1902). Chromosomal vesicles or gonomeres are present in many of the later cleavages, but in no instance have I seen any evidence that the nuclei ever divide by amitosis, as Child (1907) and Hargitt (1904, 1906) suppose to be the case in other cœlenterates.

I have followed the cleavage in *Linerges* cell by cell to the 64-cell stage and can affirm that up to this stage at least every cell divides by mitosis, while mitosis is of very frequent, if not of universal occurrence in the later divisions. In view of this fact it is needless to say that the case of *Linerges* affords no evidence whatever in favor of the view expressed by Hargitt (1906) that nuclei arise *de novo* during the cleavage of *Eudendrium, Pennaria, Clava,* and perhaps of other cœlenterates also.

After the division of the nucleus the cell-body begins to divide in the manner characteristic of the cœlenterates. The peripheral layer is thicker at the animal pole than elsewhere, as Ziegler (1903) in particular has shown for the ctenophore *Beroë*. The cleavage-furrow begins at this point and slowly cuts through the egg to the vegetal pole. The advancing edge of the cleavage-furrow (or "cleavage-head") is always rounded, and as the walls of the furrow come together behind this edge there is left a hole through the egg. In the earlier stages of cleavage this hole is elongated in the direction of the cleavage plane (figs. 8, 9, 15, 16); in later stages, as the hole approaches the periphery it becomes elongated at right angles to the cleavage plane (figs. 10, 11, 17, 18). As this advancing furrow approaches the vegetal pole the yolk is pushed aside and the peripheral layer of protoplasm from the animal pole comes into contact with that of the vegetal pole, leaving a connecting strand or bridge of protoplasm between the 2 blastomeres at the vegetal pole (figs. 11, 12). It frequently happens that after nearly reaching the vegetal pole the hole or cleavage head turns to one side (fig. 11), probably owing to the streaming of protoplasm through the bridge from one cell to the other. In this way the furrow may be turned to one side, and the daughter cells become unequal (fig. 13).

Sections of the egg before this cleavage is finished show a large cavity within the egg along the line of the cleavage-furrow (figs. 40–43). This

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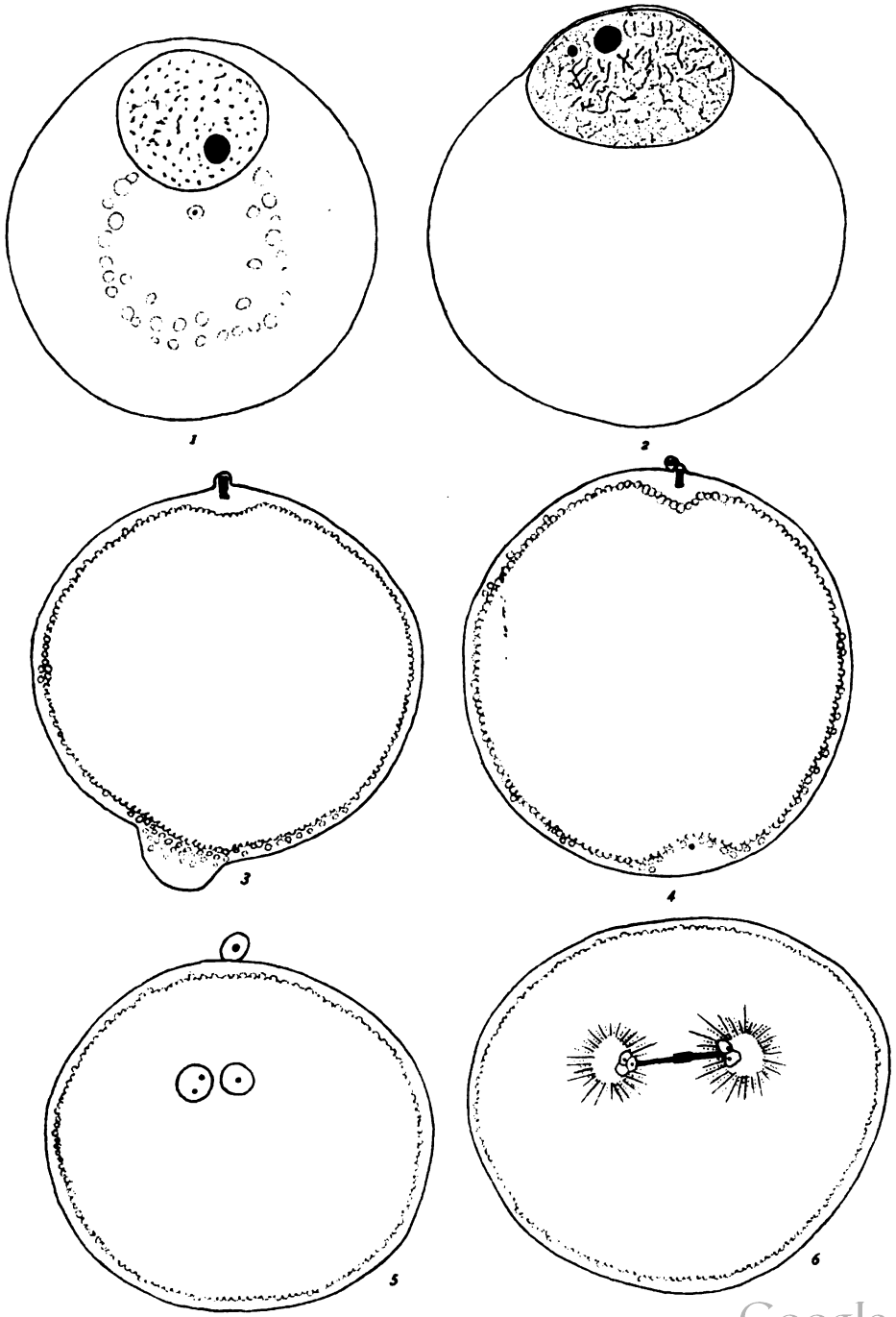
CONKLIN—LINERGES MERCURIUS



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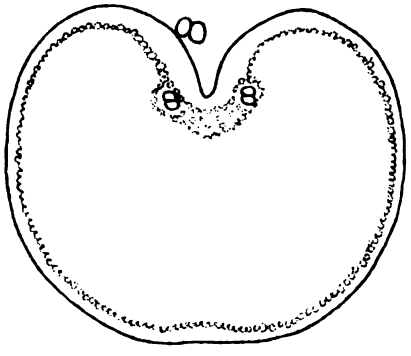

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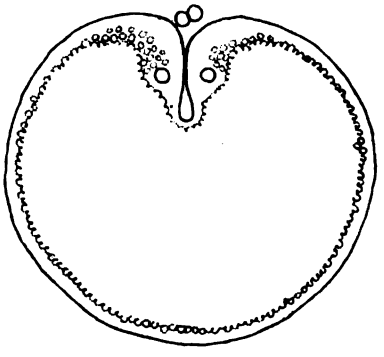

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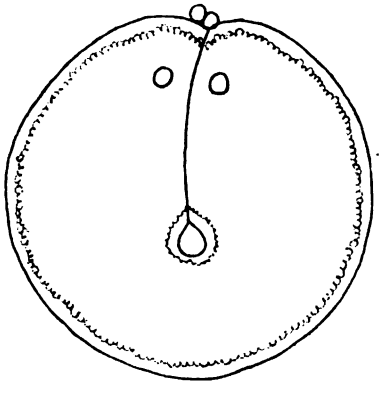

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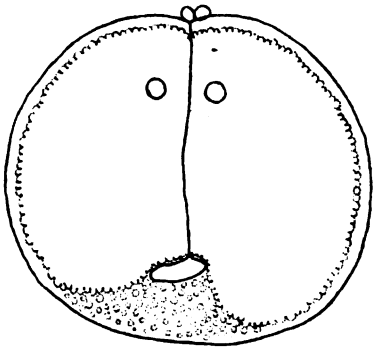

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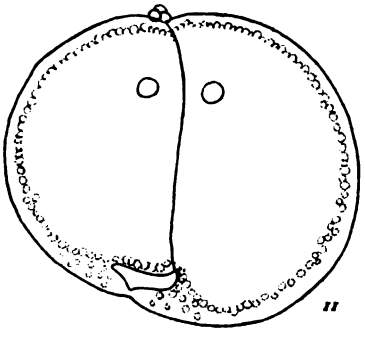

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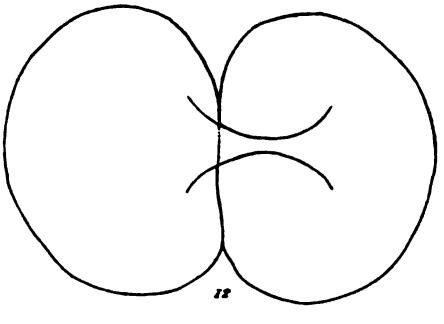

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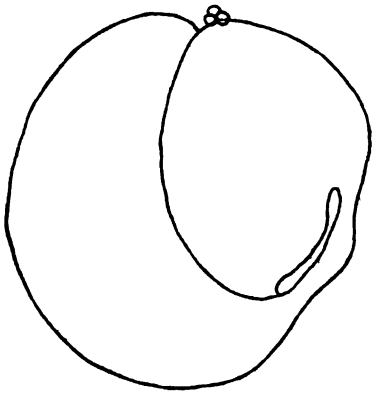

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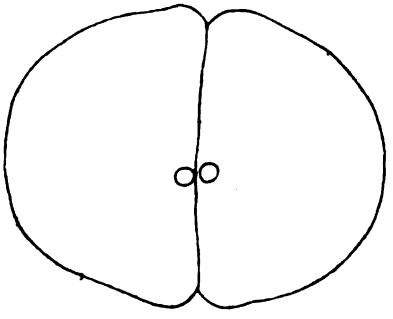

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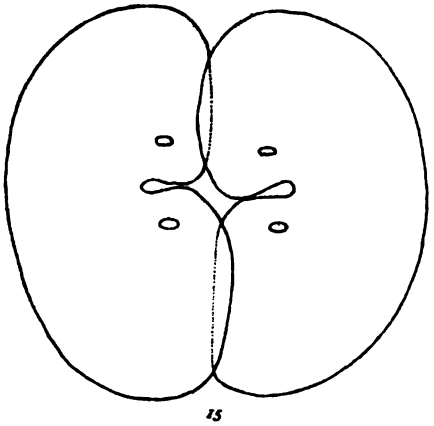

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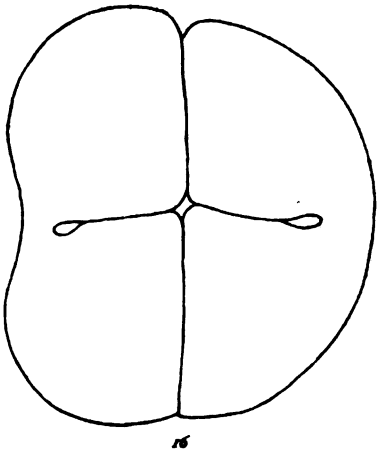

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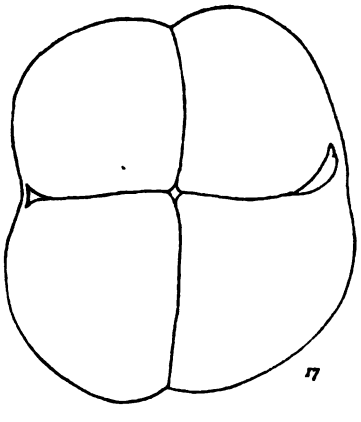

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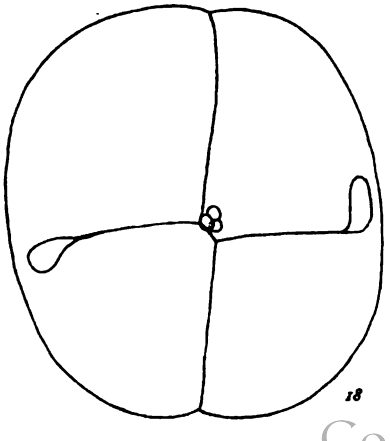

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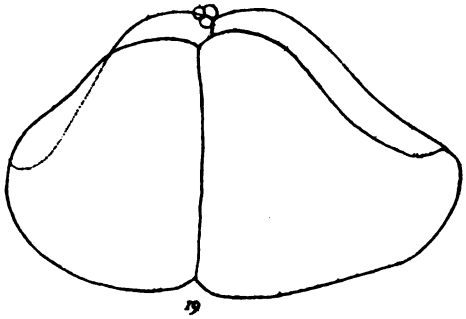

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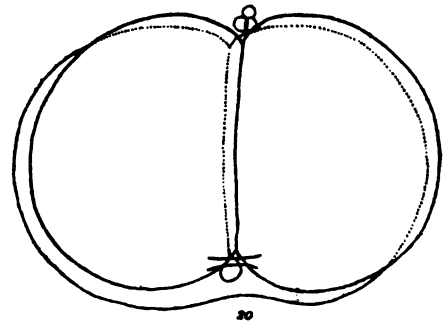

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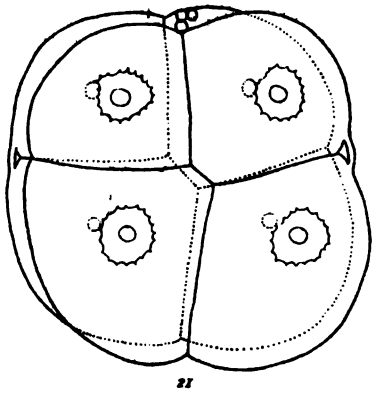

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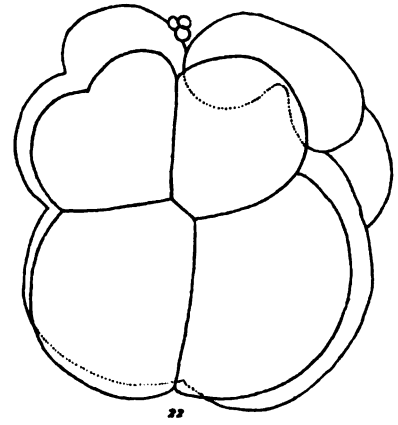

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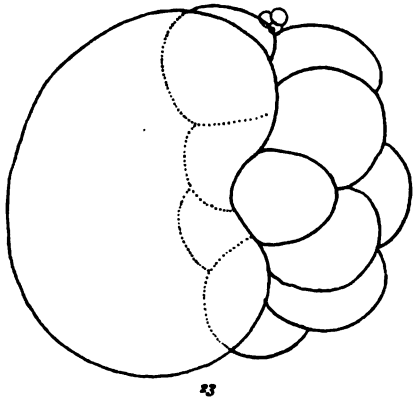

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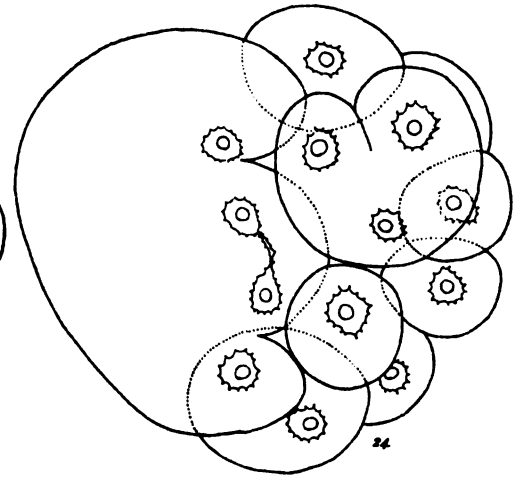

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cavity is filled with the gelatinous or fluid substance which forms the ground-substance of the central area of the unsegmented egg (*cf.* figs. 39, 40). Whether this cavity is in any sense an artifact, and if so to what extent, are questions which are difficult to answer, since the eggs are so opaque in life that their centers can not readily be seen. However, a cleavage cavity is a normal feature in the later stages of this and of most other eggs, and since the cavity present along the line of the first cleavage is directly continuous with this later cleavage cavity I conclude that it is normal and not an artifact. This cavity is found only in the region of the central area of the egg and it does not extend through the peripheral layers to the surface; furthermore, it does not communicate with the cleavage head, if one may so judge from the fact that the fluid contents of the cavity do not escape. A large part of the ground-substance of the central area of the egg escapes into this cavity during the first cleavage (fig. 41, 43), and most of that which is left in the blastomeres escapes into the cleavage cavity during the second and third cleavages (figs. 44, 45). Owing to the escape of this fluid substance from the blastomeres the latter are left much more compact and with yolk spherules more closely crowded together than in the unsegmented egg (*cf.* figs. 37, 44). Another evidence that the escape of this central ground-substance into the cleavage cavity is a normal occurrence is found in the fact that although the cleavage cavity becomes quite large, the volume of the entire egg is scarcely greater in the 8-cell or 16-cell stage than in the 1-cell stage (*cf.* figs. 37 and 46). The substance which escapes into the cleavage cavity probably represents a fluid yolk, which is gradually used up in the nourishment of the embryo.

Second and later cleavages.—The subsequent cleavages are fairly regular and in all of them, as far as I have observed, the nuclei divide by mitosis and in a manner similar to that described for the first cleavage. The divisions of the cell bodies are also similar to that of the first cleavage, though some of them merit a special description.

The second cleavage begins along the line of the first, in the center of the egg, and cuts through to the periphery (figs. 15-18). This cleavage progresses more rapidly on the side of the animal pole than on that of the vegetal pole, with the result that the connecting strand between the daughter cells is left at the periphery of the egg in the vegetal hemisphere (figs. 19, 20); later, perhaps by a slight rotation of these cells, this strand is carried still nearer to the vegetal pole (fig. 20). During this cleavage the animal hemisphere of the egg is highly arched, the vegetal hemisphere flat (fig. 19). The 4 blastomeres which result from this cleavage are approximately equal in size.

The third cleavage is equatorial and divides the egg into 8 adequal cells (fig. 21). This cleavage also begins at the center of the egg adjoining the cleavage cavity (figs. 44, 45) and cuts through to the periphery, where a connecting strand is left (fig. 21). This is the latest stage in which I

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have observed the connecting strand of peripheral protoplasm between two daughter cells. This strand is evidently the result of the unilateral constriction of the cell body, and this in turn has been held to be due to the greater amount of peripheral protoplasm on one side than on another (Ziegler, 1903). If this be true of the third cleavage as well as of the first, the protoplasmic layer should be thickest at this stage on the surface adjoining the cleavage cavity, but this is never the case. In my opinion, unilateral constriction is due in large part to the presence of a more fluid central area, as I shall show in the last section of this paper, and, therefore, when the substance of this central area disappears in the formation of the cleavage cavity and its contents, unilateral constriction during cell division also disappears.

The escape of the central ground-substance into the cleavage cavity may often be seen to take place by the separation of small globules from the inner ends of the cells, in a manner similar to that in which the so-called "plasmic corpuscles" arise in the blastocœl of *Phoronis* (Ideka, 1901) and *Terebratulina* (Conklin, 1902).

In the 8-cell stage shown in figure 44 the coagulated contents of the cleavage cavity are shown escaping at the vegetal pole, probably owing to shrinkage due to fixation. The 8-cell stage gives rise by meridional cleavages to the 16-cell stage (fig. 45). Figures 25 to 27 represent three successive cleavages of one and the same egg. Up to this stage the cleavages are normally quite regular; sometimes, however, they are more or less irregular, as shown by figures 22 to 24. These irregularities consist mainly in the temporary suppression of the division of the cell-body in one or more of the blastomeres. However, the nuclei in these blastomeres continue to divide by mitosis and the cell bodies subsequently divide (fig. 24); such eggs frequently give rise to normal blastulæ and gastrulæ. I have never observed such irregularities of cleavage in *Linerges* as have been seen by Hargitt (1904, 1906) in *Pennaria, Endendrium,* and *Clava.*

In the transition from the 32-cell to the 64-cell stage every nucleus divides by mitosis, as is shown in figure 28. In later stages the cell divisions have not been followed in detail, but I have nowhere seen any evidence of amitosis. The 64-cell stage (fig. 29) gives rise to a stage of about 128 cells (fig. 30), and the latter to a stage of double that number of cells.

Blastula and gastrula.—In a stage of about 500 cells (fig. 31) the cleavage cavity is somewhat eccentric toward the vegetal pole, and the cells at this pole are more rounded and less elongated than elsewhere; these rounded cells are endoderm. In many cases the polar bodies remain attached to the egg within the egg-membrane, and in such cases they usually lie at the pole opposite the endoderm pole, as is true of practically all animals. The animal pole of the egg becomes, therefore, the ectodermal pole of the gastrula, the vegetal pole of the egg, the endodermal pole of the gastrula.

After the 32-cell stage the entire embryo grows larger, apparently

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through the increased size of the blastocœl (figs. 29 to 32, 47, 48). At the same time the contents of the blastocœl become more fluid and stain less deeply, as compared with the earlier stages.

In a stage with about 1,000 cells (fig. 32), clear protoplasmic processes which resemble pseudopodia appear over the entire periphery of the embryo, save a small area at the vegetal pole. These processes are usually blunt-conical in shape, though some of them are very irregular. They lie under the egg-membrane, which they lift from the surface of the egg. These processes are the first steps in the formation of the cilia which ultimately clothe the entire outer surface of the larva. At first they move slowly and irregularly, but later, as they grow more slender, they vibrate in a typical manner.

Gastrulation usually takes place by invagination (figs. 33, 34, 47 to 49). The small rounded cells at the vegetal pole are pushed into the blastocœl and become the walls of the enteron, a flask-shaped cavity which opens to the exterior through the blastopore at the vegetal pole. The blastopore soon closes, so that the enteron is shut off completely from the exterior (figs. 35, 36, 50). Sometimes gastrulation takes place by the immigration of a mass of endoderm cells at the vegetal pole, and in such cases there is at first no enteric cavity in this mass of entoderm cells. Later these cells separate and arrange themselves around an enteric cavity, and the end result is the same as in cases of typical invagination. The close relationship between unipolar immigration and invagination is thus clearly shown by the occurrence of both processes in different eggs of the same animal.

In other genera of Scyphomedusæ all forms of gastrulation (invagination, immigration, delamination) occur. This fact indicates that the form of gastrulation is of no fundamental or general significance, but that it depends upon individual or environmental conditions.

Planula.—After the closure of the blastopore the embryo elongates and becomes a free-swimming planula (figs. 35, 36). The endoderm no longer forms a simple layer, but consists of a more or less irregular mass of cells, within which is the enteric cavity (figs. 35, 36, 50). In many cases (perhaps in all) several small ingrowths of ectoderm cells into the space between ectoderm and endoderm takes place (plate 8, fig. 50, text-figs. 1, 2). These ectodermal masses then become hollow. Owing to my failure to obtain material of the later stages of development I have been unable to determine their significance.

The latest stage in the development of *Linerges* which I have seen, corresponds to plate 8, figure 50 and to text-figures 1 and 2. At this stage there is no opening into the enteric cavity, though the ectodermal invagination shown at the narrower end of the larva in text-figure 2 may represent the formation of the mouth. With this stage—the free-swimming planula—my observations on the normal development come to an end.

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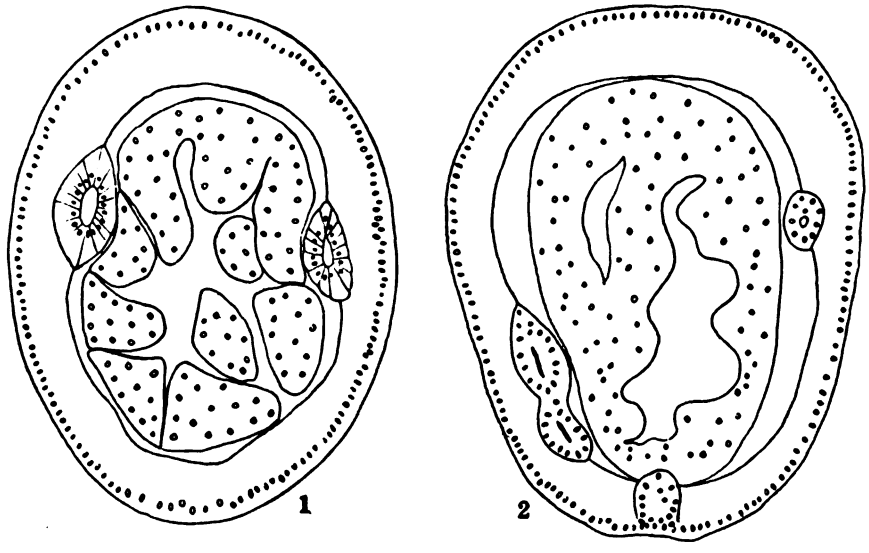

FIGS. 1 AND 2.—Longitudinal sections of the advanced planulæ, showing the columnar ectoderm, the more or less solid endoderm, containing irregular or radiating cavities, and the ectodermal invaginations which lie between the ectoderm and endoderm and are of doubtful significance. An ectodermal invagination at the narrower pole of fig. 2 may represent the stomodæal invagination.

As compared with the development of other medusæ, the entire embryology of *Linerges* is characterized by the regularity of the processes of cleavage and gastrulation; and although this regularity may suffer certain modifications, without preventing the formation of a normal planula, there is in this species none of that extreme irregularity which characterizes the development of *Pennaria* (Hargitt, 1904).

EXPERIMENTS.

Isolation of blastomeres.—My observations on the development of parts of the unsegmented egg and of isolated blastomeres are essentially similar to those of Zoja (1895) and Maas (1905). Parts of the unsegmented but fertilized egg may give rise to swimming larvæ; these are almost certainly the parts containing the egg and sperm nuclei. Isolated blastomeres, at least as late as the 4-cell stage, give rise to swimming larvæ, which are apparently normal; however the lack of clearly differentiated organs in the planula makes it difficult to determine in this stage whether the larvæ are wholly normal or not. When the egg fragments are small, or when the blastomeres are isolated at a late stage of the cleavage, the blastocœl is relatively small and the gastrulation is not normal. These results are essentially like those obtained by all investigators of the development of the Cnidaria.

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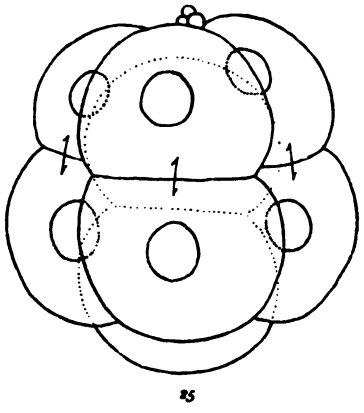

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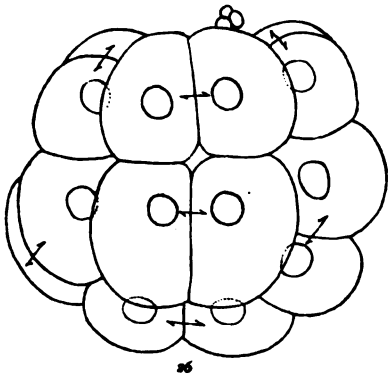

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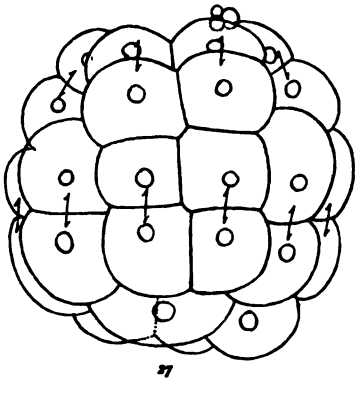

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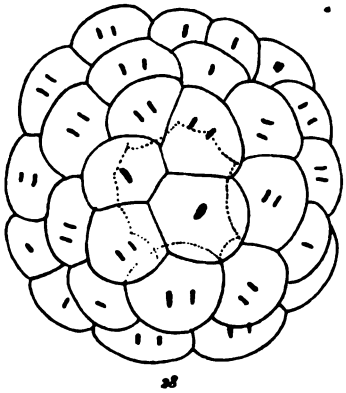

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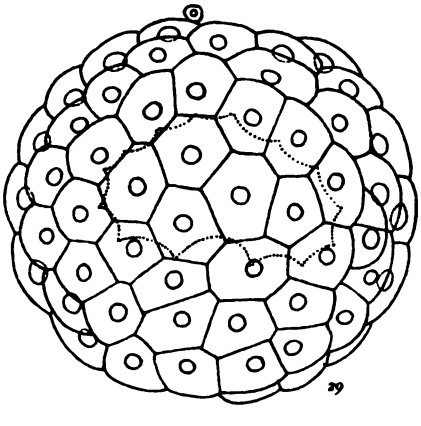

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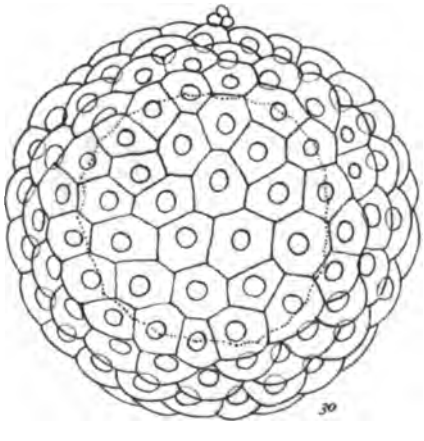

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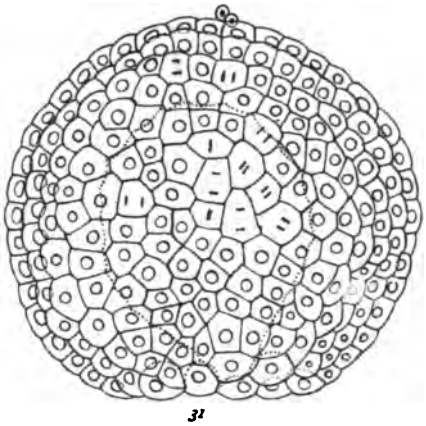

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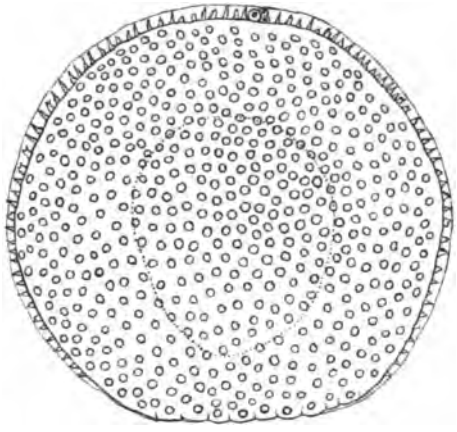

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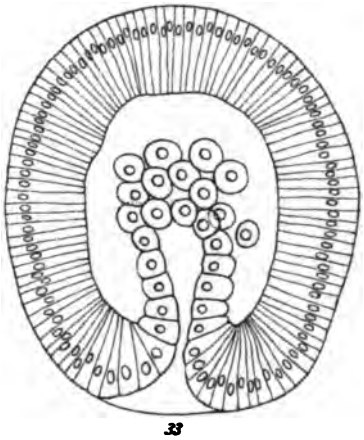

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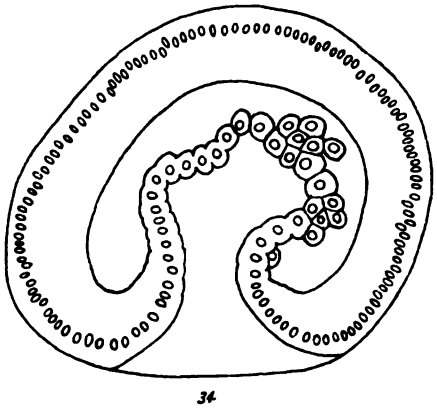

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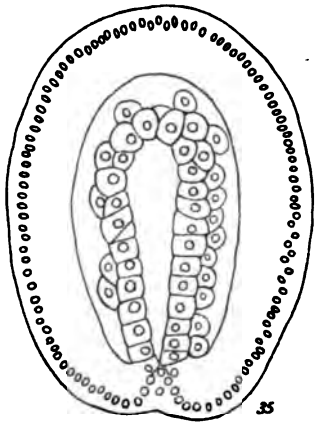

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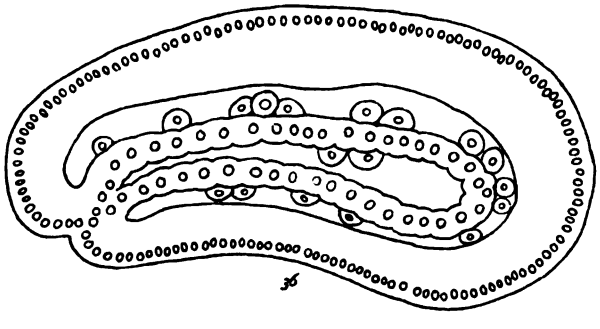

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Centrifugalized eggs.—It has been found by Lyon (1906), Lillie (1906), and Morgan and Lyon (1907), as well as by myself that the substances of the eggs of many animals may be separated into zones by means of strong centrifugal force. When the eggs of *Linerges* are centrifuged immediately after being laid, but little separation of the egg-substances is produced even if they be centrifuged at the relatively rapid rate of 12,000 revolutions per minute for 2 minutes. In later stages (just before and after the first cleavage) the substances of the egg separate much more readily.

Fertilized eggs in the stages just before and after the first cleavage when centrifuged for 1 minute at the rate of 10,000 revolutions per minute remain unaltered in structure and subsequently develop normally. If the same eggs are centrifuged at the same rate for 2 minutes the substances of the egg are separated into a clear, a blue, and a yellow zone, of which the first is the lightest and the last the heaviest. Many such eggs are evidently killed or so injured that they do not develop further, one such being shown in figure 38; others undergo irregular cleavages, which show abnormal distribution of these oöplasmic substances. In some cases irregular planulæ are formed, with an abnormal distribution of the egg-substances, and these may live and swim about for at least 24 hours. For example, in one case the clear substances formed a prominence on one side of the larva, while the remainder of the planula was blue or bluish-yellow. Whether such a planula would give rise to a normal scyphistoma was not determined, since the larvæ were not reared to this stage. And this leads me to remark that in an organism in which there are so few differentiated parts as in a planula it is practically impossible to determine with certainty whether experiments on the egg have modified its potency; only the study of later and more complicated stages could yield conclusive evidence on this point.

CONCLUSIONS.

The organization of the egg of Linerges.—The differentiations of the egg are limited to polarity and to the existence of concentric layers of differentiated oöplasm. Polarity is clearly marked in the egg before maturation, and as in practically all other animals the maturation pole becomes the aboral or ectodermal pole of the gastrula and planula, while the opposite pole of the egg becomes the oral or endodermal pole.

The egg and embryo are radially symmetrical. The cleavages are approximately equal and synchronous, and the earliest differentiation of the cleavage cells consists in the appearance of the rounded endoderm cells at the vegetal pole, while the ectoderm cells are long and narrow, forming a columnar epithelium (figs. 31–34).

Of the different concentric layers of oöplasm, the peripheral one is nearly free from yolk, and is slightly thicker at the animal pole than elsewhere. It becomes the peripheral layer of the blastula and gastrula and gives rise to the cilia which clothe the ectoderm.

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Beneath the peripheral layer is a layer of closely crowded yolk spherules in which the nuclei lie during the early and late cleavages; this yolk-rich layer constitutes the principal part of all the cells of the blastula and gastrula.

The central area of the egg contains scattered yolk spherules within a semi-fluid yolk or matrix. During the cleavage this matrix is poured into the cleavage cavity, where it seems to serve as a kind of fluid yolk for the nourishment of the surrounding cells. *The central area of the egg is thus the precursor of the cleavage cavity and its contents.*

The view expressed in my preliminary note on the development of *Linerges* (1906), that the 3 layers of the egg give rise to the ectoderm, the endoderm, and the mesoglœa is not confirmed by further study. Portions of each of these 3 layers are found in all the cells of the blastula and gastrula, and consequently in both ectoderm and endoderm; therefore these substances are not organ-forming with respect to the germinal layers. Nevertheless, each of these substances, under normal conditions, produces a specific part of the embryo. The fact that parts of the unsegmented egg or isolated blastomeres may give rise to entire planulæ may be due to the fact that such parts or blastomeres contain the oöplasmic substances of all of these 3 layers, owing to the concentric arrangement of these substances. It is not easy to isolate these substances and observe the development of each, for although they may be more or less completely separated by strong centrifugal force, they do not, in most cases, undergo further development; and the more completely these substances are separated the less capable they are of development. Nevertheless, as far as my experiments go they indicate that these oöplasmic substances are not individually totipotent.

Mechanics of cell-division.—The peculiar form of cell-division found among cœlenterates has attracted much attention. Ziegler (1898, 1903), Rhumbler (1899), and Fischel (1898, 1906) have dealt with this problem in a comprehensive manner. In brief, Ziegler holds that cell-division is brought about by the activity of the outer protoplasmic layer, the unilateral constriction being due to a heaping up of this layer to form a "cleavage head" at the animal pole; this heaping up he regards as the result of the action at a distance ("Fernwirkung") of the centrosome. Rhumbler also finds the cause of unilateral constriction in the heaping up of the peripheral layer in the cleavage head, due to the astral rays, and in the increased membrane formation in the plane of cleavage, due to the escaped nuclear substances which lie in this plane. Fischel believes that the cleavage is explicable on the assumption that the astral rays are contractile threads, and that the unilateral constriction is due chiefly to the peripheral position of the nucleus and centrosome.

In the case of *Linerges* a glance at figure 6, and the photomicrographs 38 and 42 shows that while the nuclei and centrosomes lie near the animal pole of the egg they do not lie in the peripheral layer of protoplasm. Furthermore,

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these nuclei are no nearer the periphery than in the case of many other eggs (mollusks, annelids, etc.) in which unilateral constriction does not occur. Again, the heaping up of the protoplasm at the animal pole is by no means as great as in many other animals, such as the annelids and mollusks, in which unilateral constriction does not take place. Therefore, the cause of the peculiar form of cell-division found in the early cleavage of the egg of *Linerges* and other cœlenterates is not satisfactorily explained by any of these hypotheses.

In most animals the cleavage of the egg begins at the animal pole, where the protoplasm is most abundant, and the cleavage-furrow then extends around the egg and gradually cuts in from all sides toward the center. In such cases the center of the egg is quite as firm as is the periphery. On the other hand, the center of the egg is less firm in some cœlenterates (perhaps in all) than is the periphery, and it seems probable that the unilateral constriction in the division of these eggs is partly due to this condition; for after the furrow has cut through the peripheral layers to the more fluid central area it would then progress rapidly toward the vegetal pole. This type of cleavage prevails during the first, second, and third cleavages, in fact as long as the more fluid central area is present, but with the disappearance of this area in the formation of the cleavage cavity and its contents, this type of cleavage disappears, and the ordinary type thereafter occurs. Taken in conjunction with the heaping up of the peripheral layer at the animal pole, this is, I believe, an explanation of the unilateral type of constriction of the eggs of cœlenterates.

In conclusion, I desire to express my thanks to the Carnegie Institution of Washington and to Dr. Alfred G. Mayer, Director of the Tortugas Laboratory, for the generous assistance given me while a guest of the Laboratory.

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DESCRIPTION OF PLATES.

All the figures of plates 1 to 6 represent entire eggs of *Linerges mercurius*, either drawn in the living condition or stained and mounted entire. They were drawn with the aid of the camera lucida under Zeiss apochromatic obj. 8 mm., oc. 6, at table level; in the process of reproduction they were reduced about one-third, so that as they now appear they represent a magnification of about 230 diameters. Plates 7 and 8 are photomicrographs of sections, magnified about 175 diameters.

PLATE 1.

FIGS. 1, 2. Eggs before maturation, showing the peripheral position of the large germinal vesicle.

FIG. 3. First maturation division; the maturation spindle is extremely small and apparently without centrosomes or astral rays; at the vegetal pole is a lobe of clear protoplasm which may represent the "yolk lobe" of other animals. The peripheral layer of clear protoplasm is marked off from the deeper-lying substances of the egg by the crenated line and the spherules, which represent yolk.

FIG. 4. Second maturation division; the spindle is here smaller than in the first division; within a clear area at the vegetal pole a chromatic body is found which probably represents the sperm-head.

FIG. 5. Egg showing the two germ nuclei side by side.

FIG. 6. Anaphase of the first cleavage-spindle, showing the asters, chromosomal vesicles, and connecting fibers.

PLATE 2.

FIG. 7. Appearance of cleavage furrow and "cleavage-head" at the animal pole; each of the daughter nuclei consists of two parts, the gonomeres.

FIGS. 8, 9. Further stages in the formation of the first cleavage furrow by unilateral constriction.

FIGS. 10, 11. Eggs in which the cleavage head turns to one side after reaching the vegetal pole.

FIG. 12. Egg viewed from the vegetal pole, showing the connecting strand between the two blastomeres.

PLATE 3.

FIG. 13. Egg showing the cleavage head turned still farther to one side.

FIG. 14. 2-cell stage from the animal pole, showing the blastomeres flattened against each other.

FIGS. 15–18. Successive stages in the formation of the second cleavage-furrow, showing the cleavage-head advancing from the center of the egg toward the periphery.

PLATE 4.

FIG. 19. Side view of fig. 18, in the line of the first cleavage, showing the arched condition of the egg at the animal pole and its flat appearance at the vegetal pole; the outlines of the four blastomeres are shown at the animal pole, but the cleavage-furrow has not yet reached the periphery, and hence the daughter cells are still held together here by the connecting strand.

FIG. 20. Side view of an egg at the close of the second cleavage, seen in the line of that cleavage; the connecting strands between the daughter cells are shown near the vegetal pole.

FIG. 21. 8-cell stage; side view of an egg at the close of the third cleavage, showing at the periphery the connecting strands between daughter cells.

FIGS. 22–24. Eggs showing irregular cleavage, due chiefly to the suppression of the division of the cell bodies; fig. 24 shows the nuclei and the appearance of the delayed cleavages in some of the cells.

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PLATE 5.

FIGS. 25–27. Successive stages in the cleavage of the same egg; fig. 25, 8 cells; fig. 26, 16 cells; fig. 27, 32 cells; the daughter cells are connected by arrows.
FIG. 28. Stage transitional between 32 and 64 cells; every cell shows a nucleus in some stage of mitotic division.
FIG. 29. 64-cell stage, showing (in dotted outline) the enlarging cleavage cavity.
FIG. 30. 128-cell stage, showing the cleavage cavity much enlarged.

PLATE 6.

FIG. 31. Stage of about 500 cells, showing the rounded endoderm cells at the vegetal pole; the cleavage cavity is eccentric toward this pole; several of the cells are dividing by mitosis.
FIG. 32. Stage of about 1,000 cells, showing the appearance of pseudopod-like processes from the ectoplasm, which later become cilia.
FIGS. 33, 34. Optical sections of gastrulæ, showing gastrula invagination, rounded endoderm, and mesoglœa cells, and the high columnar ectoderm cells.
FIG. 35. Optical section of a stage after the closure of the blastopore.
FIG. 36. Optical section of an elongated planula.

PLATE 7.

FIG. 37. Photomicrograph of egg after the formation of the polar bodies, showing the thin peripheral layer of protoplasm, the dense layer of yolk, and the central more fluid area.
FIG. 38. Egg centrifugalized for 1 minute at 12,000 revolutions per minute, and fixed in Flemming's fluid 6 hours later. The clear protoplasm is aggregated chiefly at the animal pole; the germ nuclei are large clear vesicles which have not undergone division; the central area is still less dense than the peripheral yolk layer.
FIG. 39. Normal egg, showing the germ nuclei in contact near the animal pole, and the substances of the egg arranged as in fig. 37.
FIGS. 40–42. Successive stages in the first cleavage of the egg, showing the furrow cutting into the central area and the formation of the cleavage cavity; one or both of the nuclei of the two cells show in all the figures.
FIG. 43. Oblique section through an egg at the close of the first cleavage, showing the cleavage cavity filled with the central matrix of the egg.
FIG. 44. Vertical section of an 8-cell stage, showing the contents of the cleavage cavity escaping at the vegetal pole.

PLATE 8.

FIG. 45. Horizontal section of an 8-cell stage, showing the mitotic spindles for the fourth cleavage; the blastomeres are partially torn apart.
FIG. 46. Section through a 32-cell stage, showing mitotic figures in some of the cells; these figures are surrounded by small, deeply-stained spherules.
FIGS. 47, 48. Vertical sections through blastulæ at the beginning of invagination; nuclei are shown in many of the cells; the cleavage cavity is greatly enlarged and its contents stain less deeply than in previous stages.
FIG. 49. Invaginate gastrula, showing the thin-walled endoderm and the thick-walled ectoderm, together with blastocœl, gastrocœl, and blastopore; in the ectoderm the cells are faintly indicated by the vertical rows of yolk spherules.
FIG. 50. Longitudinal section through a planula, showing ectoderm, endoderm, and three invaginations of ectoderm into the blastocœl; the cells of these ectodermal invaginations are quite unlike the endoderm cells, while they closely resemble those of the ectoderm.

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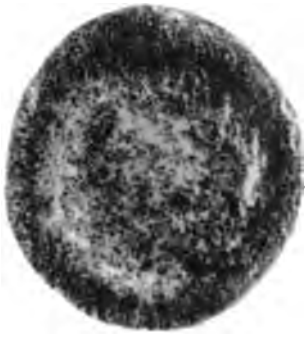

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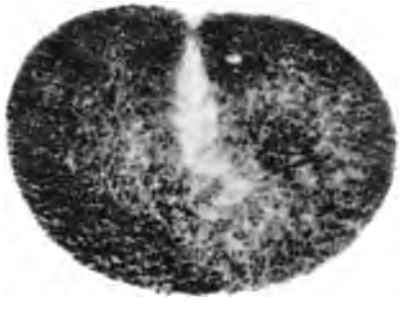

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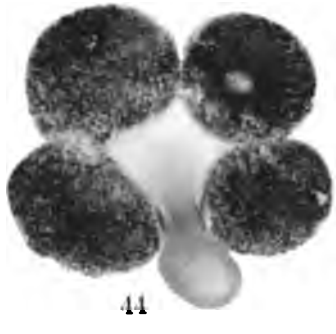

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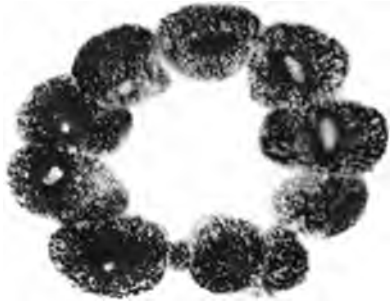

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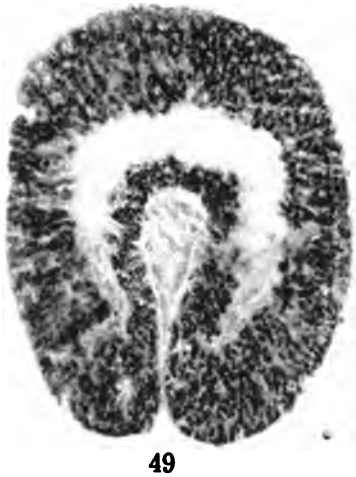

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VII. TWO PECULIAR ACTINIAN LARVÆ FROM TORTUGAS, FLORIDA.

BY EDWIN G. CONKLIN,
Professor of Zoology, University of Pennsylvania.

4 plates, 5 text figures.

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TWO PECULIAR ACTINIAN LARVÆ FROM TORTUGAS, FLORIDA.

By Edwin G. Conklin.

During a residence of about three weeks at the Marine Laboratory of the Carnegie Institution of Washington at Tortugas, Florida, in April and May, 1905, some peculiar actinian larvæ belonging to two different types were several times taken in the tow. These larvæ were usually taken toward the middle of the day, rarely in the morning or evening, which fact suggests that they come to the surface during the brightest part of the day and again sink to greater depths when the light becomes faint.

Several of these larvæ were kept during the whole of my stay at Tortugas, and Dr. Mayer, director of the station, kindly reared them and collected other specimens for me after my departure, for a further period of six weeks, but during this time no one of them became sedentary or transformed into an adult form. Again, in the summer of 1906, Dr. Mayer collected many of these larvæ and kept them in aquaria for several weeks, but no one of them underwent metamorphosis. Finally, I found these larvæ in considerable abundance at Nassau, Bahamas, in April, 1907. Although some of the individuals were quite large, no one of them had passed the larval stage. They can not, therefore, be definitely referred to any known species of Actinozoan, and although in their structure they show many adult features, they must still be regarded as larval, or at least immature forms.

When first taken these larvæ were wholly unknown to the writer, and indeed, while they were still living it was not certain to which phylum of the animal kingdom they might belong. One type bore a superficial resemblance to an annelid larva, while the other was apparently unique, but when they were killed and prepared for microscopical study it was easy to see that they belonged to the Actinozoa, and that they were immature or larval forms. On my return from Tortugas a consultation of the literature on this group showed that similar forms had been found in various tropical or subtropical seas and that they probably belong to the family of the Zoanthidæ of the order Hexactinia.

The most striking peculiarity of these larvæ is a band of locomotor cilia, which is beautifully iridescent, like the swimming-plates of ctenophores. These cilia are long and extremely numerous, and in living specimens they

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seem to adhere into a plate or membrane, as in the case of ctenophores, but after being fixed and sectioned they are frequently found separate.

In one type of larva (fig. 1) this band is longitudinal, extending from the mouth-opening along one side of the body through about two-thirds of its length; the body itself, in this form, is pear-shaped, the mouth being at the narrower end. In the other type (fig. 2) the ciliated band is circular and surrounds the body about the level of the inner end of the pharynx; at this place the body is deeply constricted, the cilia arising from the bottom of this constriction.

The first type was originally described by Semper (1867) and it has since been generally known as "Semper's larva." He found it near the Cape of Good Hope in the Mozambique Channel and on the coast of Java. The second type was also observed by Semper, but was insufficiently described by him and was supposed to be only an earlier stage in the development of the first type.

Subsequently E. Van Beneden (1890, 1898) found two specimens of the first type of these larvæ and one of the second in the material brought back by the Plankton expedition of Hensen; the former came from a region just south of the Cape Verde Islands, the latter from the Guinea Current. Van Beneden pointed out the resemblance of these larvæ to the Zoantheæ (microtype of Erdmann, 1885) in that, in common with this group, these larvæ possess a pair of perfect ventral directives, a pair of imperfect dorsal directives, and between these on each side two pairs of mesenteries, the dorsal member of each pair being perfect and the ventral member imperfect. Van Beneden made a careful study of the morphology and histology of these larvæ, reference to which will be made later. He proposed for these zoanthid larvæ, the adults of which are unknown, the following provisional names: For type I with the longitudinal band of cilia, the generic name *Zoanthella;* for type II with the circular band, the generic name *Zoanthina.*

McMurrich (1891) has also described a larva of this second type, 5 specimens of which were collected by the aid of the surface-net at Beaufort, North Carolina. He was unable to determine the adult form to which this larva belongs, but he agrees with Van Beneden that it is the larval stage of a zoanthid.

Still more recently a somewhat similar form, though showing certain notable differences, has been found and studied at Beaufort by Cary (1904), who reared the larvæ until they transformed into the adult form, which, however, he was unable to identify, although he suggests that it may be some species of the genus *Amophyllactis.*

Finally Heath (1906) has described a larva of type I which was taken near the Galapagos Islands, and which is specifically distinct from the forms described by Semper and Van Beneden. The fact that I have had

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for study more specimens than any of the investigators named and that my material was excellently fixed for histological examination has induced me to give a rather detailed description of these peculiar larvæ.

CLASSIFICATION.

As already noted, Van Beneden proposed for these two types of larvæ the generic names *Zoanthella* and *Zoanthina,* with the express statement that these names are to be regarded as provisional and that they are to be dropped as soon as it is possible to refer these larval forms to any known adult actinians. The following are the characters of these genera, according to Van Beneden:

Zoanthella: Pelagic larvæ, attaining a length of 13 mm. Body elongated, provided with a flagellar plate of distinct cilia, or with a vibratile fringe, extending parallel to the axes of the body along the anterior median line. Twelve septa, of which six are macrosepta and six microsepta, disposed as in the Zoanthariæ (microtype of Erdmann). Aboral pore present or absent.

Under this genus Van Beneden recognized two species, viz:

Z. semperi: Body cylindrical, with spiral torsion of median plane and vibratile fringe, the latter running from one pole to the other; body not incurved on ventral side at oral end; with an aboral orifice. Mozambique Current.

Z. henseni: Body elongate pyriform; large end aboral, actinosome terminal at small end; body incurved on ventral side at oral end; no aboral orifice; vibratile fringe in the upper (oral) two-thirds of body, lacking in aboral third. Guinea Current.

To these Heath (1906) has added a third species with these characteristics:

Z. galapagoensis: Body spindle-shaped; ciliated fringe slightly spiral, exposed cilia-bearing portion of fringe of much smaller extent than side in contact with mesoglœa; body not incurved; cilia of fringe not fused into membrane; no aboral pore. Near Galapagos Islands.

In almost every particular the specimens which I obtained at Tortugas and Nassau resemble *Z. henseni;* the only difference of note is that in Van Beneden's specimens the cilia of the vibratile fringe are not closely adherent into a continuous membrane, whereas in my specimens the cilia are intimately connected together in life, though they may be more or less separated after fixation. Inasmuch as Van Beneden had only two preserved specimens for study it seems probable that the separation of cilia may have resulted from the fixation, and that in life the cilia adhere closely together, as in my specimens. The Tortugas and Bahama specimens are, therefore, in all probability, examples of *Z. henseni,* and the fact that they are found in the Gulf Stream as well as in the Guinea Current indicates their very wide distribution.

The characters of the genus *Zoanthina* are indicated by Van Beneden as follows:

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Pelagic larvæ, body ovoid in early stages; a circular constriction, bearing flagellæ, divides the body into two unequal parts, an upper smaller part containing the mouth and the pharynx, and a lower larger part; 12 septa are present, 6 macrosepts and 6 microsepts, as in the microtype of Erdmann.

Z. nationalis: Larvæ longer than wide (one with 12 septa measuring 2.2 mm. in length, 2 mm. in width); ciliated furrow very deep; oral part of body attached to aboral by a sort of peduncle; no ectodermal papillæ near the mouth; no canals in mesoglœa; an orifice at aboral pole. Guinea Current.

Z. americana: Larvæ less elongated in the chief axis (one with 12 septa measures 1.4 mm. long, 1.5 mm. wide); ciliated furrow less deep; ectodermal papillæ present near mouth; canals in mesoglœa; no aboral orifice. Beaufort, North Carolina.

It is not possible to determine with certainty whether the specimens from Tortugas belong to either of these species; in fact it is not certain that the specimens obtained by Van Beneden and McMurrich belong to different species. In most regards the Tortugas specimens closely resemble both of these species, though in some respects they are different. From *Z. nationalis* the Tortugas forms differ in having no trace of an aboral pore, and if Van Beneden had not made a careful histological study of this form it might be doubted whether such a pore actually exists. As it is, it is at least possible that such a pore represents an artifact rather than a normal structure. Another difference is found in the length of the actinopharynx; in Van Beneden's specimen it does not extend as far inward as the level of the constriction; in the Tortugas specimens it does. The Tortugas form differs from McMurrich's larva only in the lack of oral papillæ and of large canals in the mesoglœa at the bases of the septa. These differences may be due to the fact that McMurrich's oldest larva was more advanced in development than any I have examined. On the whole, then, there does not seem to be sufficient ground for considering the Tortugas form as the type of a new species. Numerous specimens of *Zoanthina* were taken at Nassau, Bahamas, in April, 1907. Of these there were two different kinds; one, a small yellowish form, identical with the Tortugas species, the other frequently much larger and of a violet color. Many individuals of this latter form were as much as 5 mm. long and 3 mm. in diameter, but no one of them showed any trace of tentacles.

The larva described by Cary (1904) is evidently very distinct from the forms just named, and it is doubtful whether it can be included in the same genus; in this form the circular band consists of bristles instead of cilia, and it forms a ring open at one side instead of a closed one.

This summary shows that these larvæ have been found chiefly on the high seas in the Atlantic, Pacific, and Indian oceans. The specimens taken at Tortugas were virtually from the Gulf Stream, and it is not improbable that those obtained by McMurrich at Beaufort and by myself at Nassau were also from this same ocean current. What the habitat of the adults may be is purely a matter of conjecture.

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Fig. 1. Zoanthella henseni (?), from Tortugas, Fla. Drawn from life by Dr. A. G. Mayer. x10.

Fig. 1a. Photomicrograph of a longitudinal section of this species. The specimen is strongly flexed toward the ventral side, and associated with this is the wrinkling of the body wall at the aboral end of the ciliated band; the body wall is not wrinkled in the region of the band. x10.

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Fig. 2. Zoanthina americana (?), from Tortugas, Fla. Drawn from life. x14.

Fig. 2a. Photomicrograph of a longitudinal section of Zoanthina; although the section passes through the middle of the pharynx and cuts the ciliated groove on both sides of the mouth, the ciliated epithelium is shown on one side only. This is the only

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Transverse sections of Zoanthella 2 mm. long and 0.5 mm. wide. Photomicrographs by H. G. Kribs, taken with monochromatic blue light, of 448 μ wave-length. x125.

Figs. 3-5. Sections through the region of the pharynx.

Figs. 6-9. Sections in region of ciliated band below the pharynx.

Figs. 10-11. Sections in the aboral region, below ciliated band.

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NATURAL HISTORY.

Apparently no one save Semper has studied any of these forms in a living condition. My observations on the living larvæ, although by no means complete, may therefore be of some interest. These larvæ were taken in the surface-net, near the middle of the day, and usually in regions where the water was deep. They are quite hardy and will live indefinitely in small aquaria, though they do not grow in size or undergo metamorphosis, even though they be kept for several weeks.

Zoanthella orients itself so that the blunt aboral pole is directed upward, the pointed oral pole downward, and in this position it swims about near the surface of the aquarium, rotating on its long axis in a clockwise direction, when viewed from the oral pole. Its position and movements in the water are the results of the activity of its ciliated band, the undulations of which may be plainly seen; floating is evidently an active process, for when the cilia cease to beat the animal falls to the bottom. The rotation of the larva on its long axis is evidently due to the fact that the ciliated band runs in a slightly spiral course toward the right (clockwise) when viewed from the oral pole. Although the undulations which run from one end of the ciliated band to the other are slow enough to be easily seen, the beating of the cilia at any one level may be so rapid that the individual cilia can not be seen. Under these circumstances the ciliated band appears hazy and broader at its free edge than at its attached border.

Zoanthina larvæ usually lie on the bottom when brought into small aquaria and are motionless, except for the occasional contraction of the ciliated band. These contractions, due to the simultaneous beating of all the cilia toward the oral pole, are not unlike the pulsations of the bell of a jelly-fish, and are so slow and feeble that they do not serve to move the animal. Occasionally, however, many individuals may be found swimming rapidly near the surface of the water. This happens especially when stale water, in which they have remained for some time, is replaced by pure water. At such times these larvæ assume a conical form, the aboral pole being pointed and the oral pole truncated. The deep groove from which the ciliated band arises lies at the border of this flattened oral area and the band itself beats rapidly and violently, the stroke being toward the oral pole. Undulations or irregular contractions of the ciliated band also occur, running around the band in an anti-clockwise direction, when viewed from the oral pole. The resulting movement is quite rapid, the pointed pole being directed forward and the animal rotating in a clockwise direction when seen from the oral pole. When strongly stimulated *Zoanthina* becomes spherical in shape and the ciliated band disappears within the groove, which closes up.

Although some of the larvæ which I have studied are large and well-developed, no food has ever been found in the cœlenteron; even diatoms and microscopic algæ are lacking. Occasionally fine threads of a coagulum

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are found in the cœlenteron, but judging by the considerable number of specimens which I have sectioned I am inclined to believe that solid food is rarely ingested. One of these specimens (figs. 12-18), which was 3.5 mm. long and 1.2 mm. in diameter, after fixation and preservation for a year in alcohol, had no mouth opening, so that it could have taken no solid food, but its considerable size would suggest that it must have grown a good deal beyond the size of the egg. To a considerable extent this growth may be due to the formation of the hollow cœlenteron and to the absorption of water, as Davenport showed to be the case in the early growth of the tadpole, but it is possible that in this case nutriment may be received from another source. In all of these larvæ there are considerable numbers of large round cells with dense nuclei and with yellowish-green granules in the cytoplasm. These are symbiotic algæ, resembling *Zoöxanthella,* and it is quite possible that they play an important part in the nutrition of the larvæ. These algæ occur in both *Zoanthella* and *Zoanthina* and in both the ectoderm and endoderm, though they are more numerous in the latter layer; they also occur in the youngest larvæ, with imperforate mouth, as well as in the oldest ones. The fact that these larvæ are found at the surface at a period of the day when most pelagic larvæ have settled to deeper and darker levels may be associated with the metabolism of this symbiotic alga, and it may be that if these larvæ had been kept in aquaria which were exposed to bright sunlight the later stages in their development might have been secured.

MORPHOLOGY.

Zoanthella.—The general shape of this larva has been sufficiently described already and may be seen in plate 1, figs. 1, 1*a*. The color is a greenish or brownish yellow, mottled with darker spots, and it seems probable that this general color is due, in part, to the large number of *Zoöxanthellæ* present in the body-walls. The size of the larvæ varies within wide limits, as Van Beneden has remarked, and the size is not in itself a measure of the degree of development. My smallest specimen is 2 mm. long and 0.5 mm. wide (plate 2), but it is much further developed than another specimen 3.5 mm. long and 1.2 mm. wide (plate 3). The largest specimen which I have measured is 8 mm. long and 2 mm. wide after having been fixed and cut into longitudinal sections. Many specimens were sectioned without having been measured, and accurate measurements of these can not now be given, but their relative sizes may be determined by the number of sections in each series, since the sections are of uniform thickness; these vary from 250 to 600 in number.

In none of the larvæ which I have seen is there any trace of tentacles or oral papillæ. In *Zoanthella* the mouth and actinopharynx is formed at a relatively late stage. In the larva, 3.5 mm. long, shown in plate 3, the pharynx has just begun to invaginate and the mouth is still imperforate,

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although all of the macrosepta are well-developed and the microsepta are already present. In the oldest of these larvæ, 8 mm. in length, the pharynx is only 1.1 mm. long. In cross-section the pharynx of *Zoanthella* is quadrilateral in shape, the four sides of the quadrilateral being incurved toward the center (plate 2, fig. 3). The longitudinal plications of the walls of the pharynx correspond in position to the primary septa (macrosepta) and below the pharynx these plications are directly continuous with the mesenterial filaments of these septa (plate 3, figs. 4–6).

The septa consist of three pairs of macrosepta and three of microsepta, and, as Van Beneden has shown, their arrangement and sequence corresponds to that of the Zoantheæ (microtype of Erdmann), *i. e.*, the dorsal directives are imperfect, the ventral are perfect, and of the two remaining pairs on each side the dorsal member of each pair is perfect and the ventral one imperfect. Van Beneden holds that the order of appearance of the septa, as judged by their size, is for the macrosepta: 1, lateral; 2, dorsal; 3, ventral; and for the microsepta: 4, dorso-lateral; 5, ventro-lateral; 6, dorsal directives. In the youngest *Zoanthella* which I have sectioned the dorsal macrosepta are smaller than either of the other pairs (plates 2 and 3), and judged by the standard hitherto used they are the last-formed of the macrosepta. Three pairs of microsepta are present in these youngest larvæ and they are all about equal in size.

The macrosepta are triangular in cross-section, as shown in plates 3 and 4 and text-fig. 4, the base of the triangle lying at the central border of the septum. To this thickened central border the cylindrical mesenterial filaments are attached. A similar condition was observed by Heath in *Zoanthella galapagoensis,* but Van Beneden does not figure or describe it in the other species of this genus.

In the interspaces between macrosepts and microsepts are endodermal thickenings, which are sometimes as prominent as the septa themselves. These thickenings consist of vacuolated endoderm cells and in the younger larvæ (plate 3) they fill up a large part of the cavity of the cœlenteron, especially at the aboral end; in the older larvæ (text-fig.) they are much less voluminous, probably representing the remains of the primitive endoderm which, in earlier stages, filled the entire enteron.

Zoanthina.—The shape of this larva varies greatly with different stages of contraction; it may be elongated as shown in plate 1, figure 2, or contracted so that the oral-aboral axis is no longer than the transverse one (plate 1, fig. 2*a*, text-fig. 1). In some specimens the oral portion of the body, in front of the ciliated band, is relatively much larger than in the specimen represented in plate 1, figure 2. In general this larva is shorter and stouter than *Zoanthella.* In color it resembles the latter, being of a light brownish-yellow, mottled with darker spots; some of the Nassau specimens are of a violet tint. My smallest specimen of this genus is about 1 mm. long and 1.2

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mm. wide, while the largest is 4.3 mm. long and 2 mm. wide. These measurements were made on material which had been preserved in alcohol for a year.

In all of my specimens of *Zoanthina* the mouth and pharynx are fully formed and the size of the septa and absence of the endodermal thickenings between the septa indicate that these larvæ are more advanced in develop-

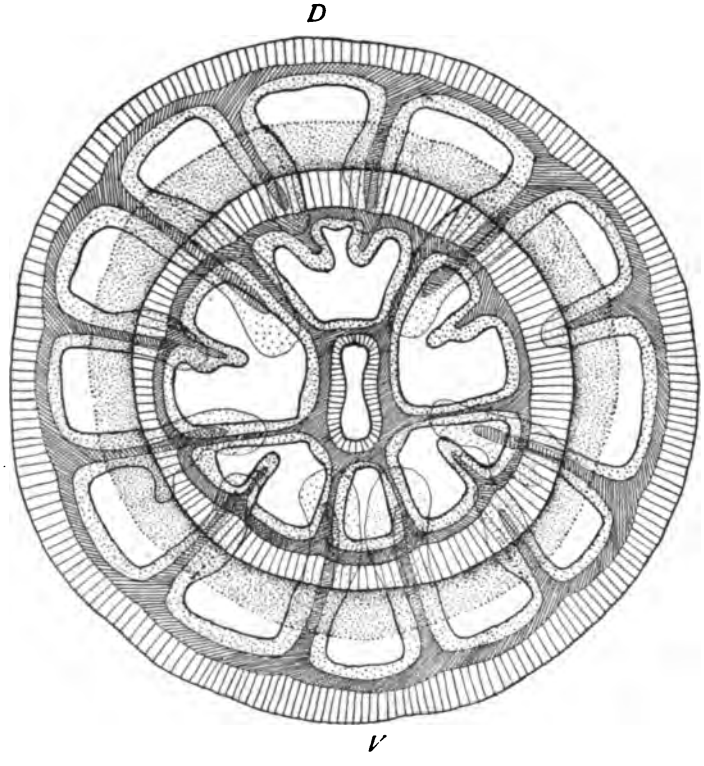

FIG. 1.—Entire specimen of *Zoanthina*, viewed from oral pole; specimen stained and mounted in balsam. Ectoderm shaded by radial lines, mesoglœa by oblique lines, and endoderm by light stippling; ciliated groove deeply stippled.

ment than those of *Zoanthella* which I have studied. The mouth-opening is round in outline, but the pharynx is compressed laterally, as shown in text-figure 1. In this genus the pharynx extends inward at least as far as the circular constriction, about one-third the length of the entire body (plate 1, fig. 2*a*). The walls of the pharynx are thrown into longitudinal plications, which become continuous with the mesenterial filaments of the macrosepta (plate 4), as in *Zoanthella*.

The septa are relatively larger than in *Zoanthella*, and this is especially true of the microsepta, but Van Beneden holds that their arrangement and order of appearance are the same in the two genera, *i. e.*, the dorsal direct-

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ives are imperfect, the ventral are perfect, and of the two remaining pairs on each side the dorsal member of each pair is perfect and the ventral one imperfect, while the order of appearance is, for the macrosepta, 1, lateral; 2, dorsal; 3, ventral; and for the microsepta, 4, dorso-lateral; 5, ventro-lateral; 6, dorsal directives.

McMurrich agrees with Van Beneden that the arrangement of the septa of *Zoanthina* is characteristic of the *Zoantheæ,* but he suggests that the sequence observed by Van Beneden is really due to the retardation of the development of the dorsal directives, which should, according to his view, stand fourth in the order of development.

In all my sections of *Zoanthina* the dorsal directives are smaller than the other microsepta (text-fig. 1 and figs. 24, 25), and if the order of appearance is to be judged by the relative sizes of the septa, the dorsal directives are the last to appear of these 6 pairs. Therefore, my observations as to the sequence of the septa in *Zoanthina* agree with the conclusions of Van Beneden.

The individual septa are not triangular in cross-section, as in *Zoanthella;* on the contrary they are nearly as wide at the base as at the free border, and they all show a greater thickening on one side of the mesoglœa than on the other (figs. 24, 25 and text-fig. 1). In the ventral and dorsal directives these thickenings face the median plane, in the laterals and ventro-laterals they face the ventral side, in the dorso-laterals and dorsals they face the dorsal side.

Although the microsepta are well-developed, the macrosepta only are united to the pharynx (fig. 21). Van Beneden found that the septa in the oral and aboral portions of the body were not continuous through the region of the constriction. In the Tortugas specimens the septa are small in this region, but they are not interrupted (figs. 22 and 23). Sections through the outer fold of the ciliated groove show the presence of 12 pockets, formed by the 12 septa (fig. 23).

HISTOLOGY.

In most respects the histological character of these two types of larvæ is similar, though there are certain minor differences.

Ectoderm.—The ectoderm consists of greatly elongated cells, among which are numerous cell-spaces. At the free border of the epithelium no cell-spaces are visible and the cells are here more darkly stained than at deeper levels. The inner ends of the cells are narrow and apparently few of them run through the entire epithelium from the free border to the mesoglœa. Among the epithelial cells are nematocysts of two types, smaller ones which lie near the surface, in fact with one end of the nematocyst at the free border of the epithelium, and much larger ones which lie at a deeper level. In text-figure 2, which is a section through the ectoderm and mesoglœa of *Zoanthella,* both kinds of nematocysts are shown and at the base of

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the epithelium near the left side of the figure is a nematoblast from which the larger type of nematocysts is formed.

Two types of gland-cells are also to be found in the ectoderm; one of these consists of elongated fusiform cells containing many small granules

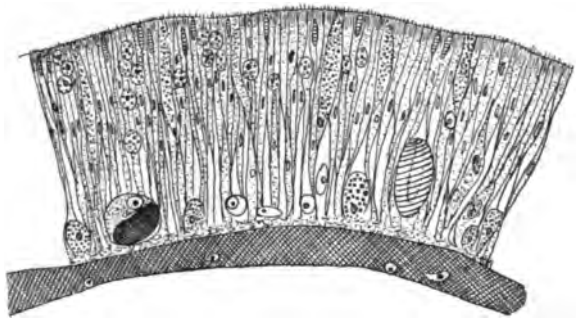

FIG. 2.—Section through body-wall of *Zoanthella*, showing character of ectoderm and mesogloea. × 333.

and lying with the outer end near the free border of the epithelium; the other type consists of rounded cells containing larger granules lying at the base of the epithelium; these cell granules stain intensely with plasma stains (text-fig. 2). In *Zoanthina* there are gland-cells which stain intensely with nuclear stains and which constitute a third type (text-fig. 5).

Other cellular elements of the ectoderm are the Zoöxanthellæ, which are especially abundant in *Zoanthella;* these are small round cells with dense nuclei and with yellowish or greenish chromatophores. They are found most abundantly in the outer portion of the ectoderm.

At the base of the epithelium and adjoining the mesoglœa is a layer of fine fibrils which run in all directions and which consequently appear in sections as fine dots or short fibers. These are probably the fibrillar bases of the epithelial cells.

The description just given applies to the general ectoderm of the larvæ. In the region of the ciliated band this epithelium is remarkably altered. The nematocysts and gland-cells are here lacking, while the ordinary ectoderm cells are replaced by exceedingly slender elongated cells (text-fig. 3). The nuclei of these cells lie in the deeper part of the epithelium, while the cell-bodies consist of slender filaments which are continued from the nuclei to the periphery of the epithelium and then into long flagellæ, which constitute the vibratile band. The free border of the epithelium is marked by a faint line. It seems probable that this line marks a plane along which the various cell filaments fuse together. The filaments are apparently as numerous within the epithelium as without it and they are more numerous and more powerfully developed than in any other epithelium I have ever seen. At the base of this ciliated epithelium are a few rounded cells, some of which

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are plainly zoöxanthellæ, and between the nuclei of the ciliated cells and the mesoglœa is a finely granular or fibrillar layer, which resembles the fibrillar layer at the base of the ordinary epithelium. The boundary between the ciliated plate and the ordinary ectoderm is sharp and distinct and there are apparently no transitional cells between the two. The ordinary epithelium does not overgrow the ciliated band at its margins as in the case of *Zoanthella galapagoensis*. In the latter species the ciliated cells are much longer, as compared with the ordinary ectoderm, than in the Tortugas species.

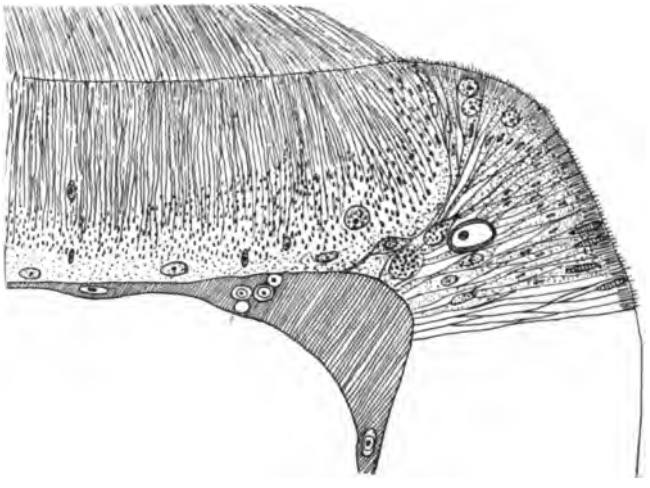

FIG. 3.—Section through ciliated band and adjoining ectoderm of *Zoanthella*. Flagellated cells extremely long and slender, appearing like masses of spermatozoa; among them a few larger cells, and at base of epithelium is a granular zone. Mesoglœa is very thin beneath ciliated plate, but at edges very thick. × 333.

In *Zoanthina* the ciliated band is circular and of nearly uniform width; in *Zoanthella* it is longitudinal and varies much in width, being widest in the middle and narrower at either end. In some specimens of *Zoanthella* the band is apparently double, being divided along its middle by a line of clear, non-ciliated cells (figs. 13-16). I was at first inclined to the opinion that the forms with the divided band were specifically distinct from those in which it is not divided, but further study makes it probable that this is only an individual variation. A similar splitting of the ciliated plate in its aboral portion was observed by Heath in the Galapagos specimen.

The epithelium of this ciliated band has essentially the same structure in the two types of larvæ. It is characterized by extremely small and compact nuclei, which resemble the heads of spermatozoa, and by very long, slender cell-bodies, every one of which starts from a nucleus and runs as a fibril to the periphery of the epithelium and is then continued into the free

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flagellum. The iridescence of the ciliated band is due to the great number of these parallel flagellæ, which diffract light like the lines of a fine grating.

I have not been able to distinguish muscle or nerve cells in the ectoderm, though the basal fibrillar layer may represent processes from one or both of these kinds of cells.

The epithelium of the pharynx is more compact than that of the general ectoderm and it contains a larger number of gland-cells; consequently it stains more deeply than does the general ectoderm.

Endoderm.—With the exception of the mesenterial filaments the endoderm stains less deeply than does the ectoderm and the cell outlines are less distinct. Indeed, the general endoderm consists of a spongy layer in which

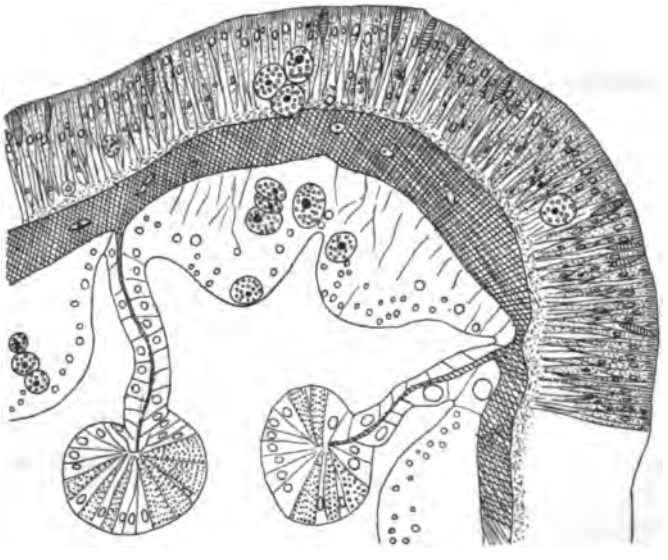

FIG. 4.—Cross-section through body-wall of *Zoanthella,* showing ectoderm, mesoglœa, endoderm, and two septa with mesenterial filaments; the gland-cells of the latter are especially evident. × 333.

are numerous nuclei near the free border, and zoöxanthellæ in the deeper portion of the layer, but in which cell boundaries are not distinct, except close to the free border. In *Zoanthina* the cell boundaries and nuclei are more distinct than in *Zoanthella,* and along the free border they form a definite epithelium, but in the deeper portions of the layer there are few nuclei and no cell outlines save those of the symbiotic algæ, and of a few wandering or amœboid cells (text-figs. 4 and 5).

The mesenterial filaments are rich in gland-cells filled with a granular secretion, while adjoining epithelial cells contain no granules, text-fig. 4.

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Transverse sections of Zoanthella 3.5 mm. long and 1.2 mm. wide. Photomicrographs by H. G. Kribs, taken with monochromatic blue light of 448 μ wave-length. x75.

Fig. 12. Section through the oral region, showing endoderm filling the coelenteron; at this stage the mouth is imperforate and the pharynx has not formed.

Figs. 13-17. Sections through the region of the open coelenteron; the ciliated band is plainly divided down the middle.

Fig. 18. Section through the aboral region, showing the spongy endoderm filling the entire coelenteron. At various places cells

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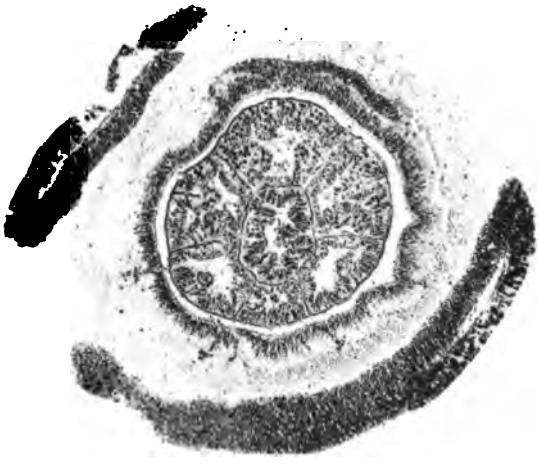

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Transverse sections of Zoanthina americana (?), 1.8 mm. long and 1.2 mm. wide. Photomicrographs by H. G. Kribs, taken with monochromatic blue light of 448 $\mu\mu$ wave-length. x75.

Figs. 19-21. Sections through portion of body on oral side of ciliated groove.

Fig. 22. Section through ciliated groove, showing a portion of the outer wall of the groove.

Fig. 23. Section through deepest part of ciliated groove, showing twelve endodermal pockets in outer wall of groove.

Figs. 24-25. Sections through the aboral part of the body. The endoderm cells contain many small round bodies, the Zooxanthellæ.

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MESOGLŒA.

The mesoglœa is generally thicker in *Zoanthella* than in *Zoanthina* and varies considerably in thickness in different parts of the same larva. In both types of larvæ it is thickest in the aboral portion of the body and thinnest beneath the ciliated band. The extreme thinness of the supporting lamella in the region of the ciliated band as contrasted with its thickness elsewhere is well shown in text-figure 3 and in plates 2 and 3. The same figures show that in *Zoanthella* this layer is thinner opposite the point of origin of septa than in the region between septa, while in *Zoanthina* the reverse is true. Cells and canals are found within the mesoglœa in both larvæ, though they are more abundant in *Zoanthella*. There is considerable evi-

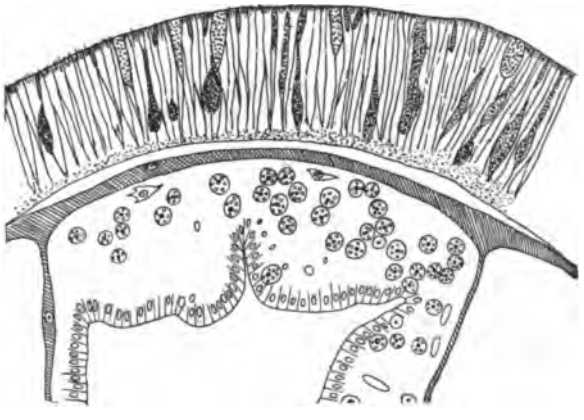

FIG. 5.—Cross-section through body-wall of *Zoanthina*, showing mesoglœa and endoderm. × 333.

dence in favor of the view of Van Beneden that the mesoglœa is in life quite soft and that the cells found in it are wandering cells and the canals merely the tracks of these cells.

In my oldest specimen of *Zoanthina* the mesoglœa in each of the macrosepta is drawn out into many fine branches on the thicker side of the septum, thus giving support to the longitudinal muscles of the septa. In *Zoanthella* the flexure of the body toward the ventral side gives evidence of the presence of strong longitudinal muscles along that side, though I have not been able to distinguish them in my sections. Van Beneden has seen and described these muscles in the specimens which he studied.

In none of the specimens which I have examined were there any embryos within the cœlenteron, such as Van Beneden discovered in *Zoanthina nationalis*. These embryos he shrewdly concludes were merely ingested by an older embryo, while all were contained within a cœlenteron of the viviparous parent. If this is the true explanation of their presence in Van Beneden's specimen, it may be concluded that a more extensive study of the

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zoanthinas found at Tortugas will show that some of these contain embryos also. In the oldest of the larvæ which I have examined there is not a trace of germ-cells and they can not therefore be capable of sexual reproduction.

Although these peculiar larvæ have been taken only a few times and then in widely separated parts of the earth; they are certainly not extremely rare, as their abundance at Tortugas and at Nassau shows, and I do not doubt that with the excellent facilities now afforded at the Tortugas Laboratory, some investigator more fortunate than myself will be able to observe their transformation into the adult form, and thus to determine beyond any doubt their systematic position.

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VIII. THE BEHAVIOR OF NODDY AND SOOTY TERNS.

BY JOHN B. WATSON,
Professor of Experimental and Comparative Psychology, The Johns Hopkins University.

11 plates, 2 text figures.

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THE BEHAVIOR OF NODDY AND SOOTY TERNS.

By John B. Watson.

INTRODUCTION.

During the spring of 1907, on the invitation of Prof. Alfred G. Mayer, Director of the Marine Biological Laboratory of the Carnegie Institution of Washington, I spent three months upon Bird Key, a small island belonging to the Dry Tortugas group.[1] The specific object of my stay was to observe as far as possible the details of the lives of the noddy terns (*Anous stolidus*) and the sooty terns (*Sterna fuliginosa*) during their nesting season on that island.

My thanks are due first of all to Professor Mayer for his unfailing kindness in liberally supplying my needs upon the island. Bird Key is uninhabited and is some distance from the key upon which the Biological Station is located. Since I lived upon the island, it was necessary to bring all supplies and apparatus from the laboratory. During this period I was supplied with a motor-boat and a servant. My thanks are likewise due to the Audubon Society, which not only rendered me financial assistance for acting as warden of the island, but also allowed me complete control of the birds. On an island as small as Bird Key it would have been difficult to have carried on the work if my authority had been divided with that of a regular warden.

Mr. Carl Kellner spent many trying hours with me in attempting to photograph the birds in action. Owing to the peculiarities of the climate and to the extreme rapidity of the characteristic movements of the birds, we had scant success in our efforts. Our interest was not so much in obtaining good photographs of the birds, but rather centered around the portrayal of their activities. Many hundreds of photographs were taken, but many of the most interesting exposures, which were often made after hours of waiting, failed to develop properly for one reason or another.

As will be seen by reading the present report, the nature of all the work has been preliminary. Indeed, if I were convinced either that I myself or some one else could immediately take up the work, I should cheerfully delay publication until a fuller account of the activities of the birds could be given. But since the immediate continuation of the work is not assured, and since

[1] In this connection I wish to thank Prof. James R. Angell for arranging for me a three months' leave of absence from the University of Chicago, with which institution I was connected at the time the present research was made.

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work of this kind is more or less "impressionistic," the attempt is here made, while the material is still fresh in my mind, to enumerate some of the more important problems to be found in the study of these birds and to set forth my tentative efforts to solve them.

OBSERVATIONS UPON THE INSTINCTS AND HABITS OF TERNS DURING THE NESTING SEASON.

A GENERAL DESCRIPTION OF THE TWO SPECIES OF TERNS.

THE NODDY TERN (ANOUS STOLIDUS).

The noddy tern is described by Saunders,[1] as follows:

Adult Male in Breeding Plumage.—Forehead nearly white at the base of the bill, passing on the crown into lavender-gray, which deepens on the neck into lead color; lores and orbital region black with a faint whitish superciliary streak; upper parts chiefly dark-brown, the primaries, tail feathers, and their shafts nearly black; underparts dark brown on the abdomen and breast, passing into deep lead color on the throat; bill blackish; tarsi and toes reddish-brown, fully webbed, webs ochraceous. Total length about 16 inches, culmen 2.1, wing 10.25 to 11, tail 6 to 7, the fourth feather from the outside the longest, tarsus 1, middle toe with claw 1.55.

Adult Female.—Very similar, but as a rule somewhat browner on the shoulders and with less lead color on the throat, slightly smaller and with a weaker bill.[2]

Hab. Tropical and juxta-tropical America; chiefly on the Atlantic side, but also on the Pacific in Mexico and in the central region; Atlantic down to Tristan da Cunha (breeding); intertropical African and Asian Seas, up to Yeddo; Australasia down to about 35° S.; Islands of the Pacific up to Laysan, etc., and as far as Sala y Gomez, 105° W.; also Chatham I., Galapagos (*fide* Ridgway), but not on the coasts of Peru or Chile. Breeding, as a rule, where found. Once obtained off the south coast of Ireland.

THE SOOTY TERN (STERNA FULIGINOSA).

Rothschild's[3] description of the sooty is as follows:

Adult.—Forehead, sides of head, and entire lower parts, including lower wing coverts, white with a very delicate bluish tinge on the abdomen under wing-coverts and under tail-coverts when the birds are alive or quite fresh. Lores and upper parts, including the hind neck [which is whitish in *H. anoestheta* (Scop)], uniform sooty brown. Primaries black, but the shaft and outer web of the first primary white below, except on the outermost tip. Tail-feathers sooty-black; all the shafts white below, and the shafts of the outer pair, as well as their outer web and basal part of inner web, white. Total length about 17 to 17.5 inches, wing 11.6 to 12, outer rectrices (if not abraded) 7.5 to 8, central pair 3, culmen 1.7 to 1.8, tarsus 0.85. (Specimens from America and Kermadec Islands are exactly similar.) Iris dark-brown, bill and feet black.

Hab. Tropical and juxta-tropical seas, breeding wherever suitable islands and reefs exist; occasionally wandering to Maine in North America, and to Europe, even as far as England. Almost unknown on the South American side of the Pacific; otherwise very generally distributed.

[1] Catalogue of the Birds of the British Museum, vol. xxv, pp. 136–140.

[2] I could not find any difference in appearance between the males and females. The two sexes in life are indistinguishable. This applies to both noddies and sooties.

[3] Avifauna of Laysan, etc., p. 39.

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On account of the wide distribution of these two species of birds, of their great numbers, and of their habit of assembling on islands during their nesting season, frequent incidental reference to them is to be found in the writings of naturalists. Saunders gives a fairly complete reference to this literature.

Extended statements concerning the instincts and habits of these birds are not extant. Dr. Thompson[1] gives the most comprehensive statement concerning their habits. His observations, like my own, were made upon Bird Key. The statements in his paper are apparently made upon the basis of intermittent visits to the island and are not always trustworthy. This is not to be wondered at when we consider the complexity of the life of the birds and the limited time which was at Dr. Thompson's disposal.

Descriptive and none too exact statements of the nesting behavior of the birds may be found in Henshaw[2] and in Rothschild.[3] In the latter, most of the observations were made by the naturalist Palmer. The work of Walter K. Fisher[4] is especially worthy of mention.

The above references bear only in a general way upon my own studies. In many cases, the observations to be found in them do not agree with my own. I am not able to account for these discrepancies. The account of the instincts and habits of these birds given here is made largely upon the basis of my own observations.[5]

Nearly all of the statements concerning the habits of these birds, like my own, refer to the nesting season. So far as I know to the contrary, almost nothing is known of their life outside of this period. Many of the reactions during the nesting season could be understood more easily if we knew the complete history of their life-cycle.

GEOGRAPHICAL SITUATION AND HISTORY OF THE PRESENT COLONY OF TERNS.

Bird Key is a small coral island about 300 yards wide (east and west) by 400 yards long (north and south). It is 65.8 statute miles due west from Key West. The island is partially sheltered on the east and on the northeast by a coral reef (fig. 1). Northeast of the island, about 1.125 statute miles distant, stands Fort Jefferson, now practically deserted. Still farther to the northeast other low coral islands are to be found. Loggerhead Key lies

[1] Bird Lore, vol. v, 1903, p. 77 ff.
[2] Birds of the Hawaiian Islands, etc., 1902.
[3] *Op. cit.*
[4] Birds of Laysan and the Leeward Islands, Hawaiian Group. Bull. U. S. Fish Commission, vol. XXIII, 1903, pp. 767–807.
[5] As examples of differences in observations I cite the following: One writer speaks of seeing these terns "swimming in the water." During my three months' stay I never saw one of these birds in the water, except by accident (see fig. 26, plate 10), and then the bird, if the tide is against it, can never reach the shore, so poorly does it swim. Another statement is to the effect that these birds are often seen flying at night at great distances from the shore. My own observation is to the effect that the birds return to the island at night and leave it at daylight.

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about 4 statute miles to the west of Bird Key. Immediately outside of these islands is to be found the water of the Gulf of Mexico. The situation of the island shows that it is adequately protected from all but the severest southwest storms. The Tortugas as a whole are rarely subject to heavy storms during the nesting period of the birds. During the past season

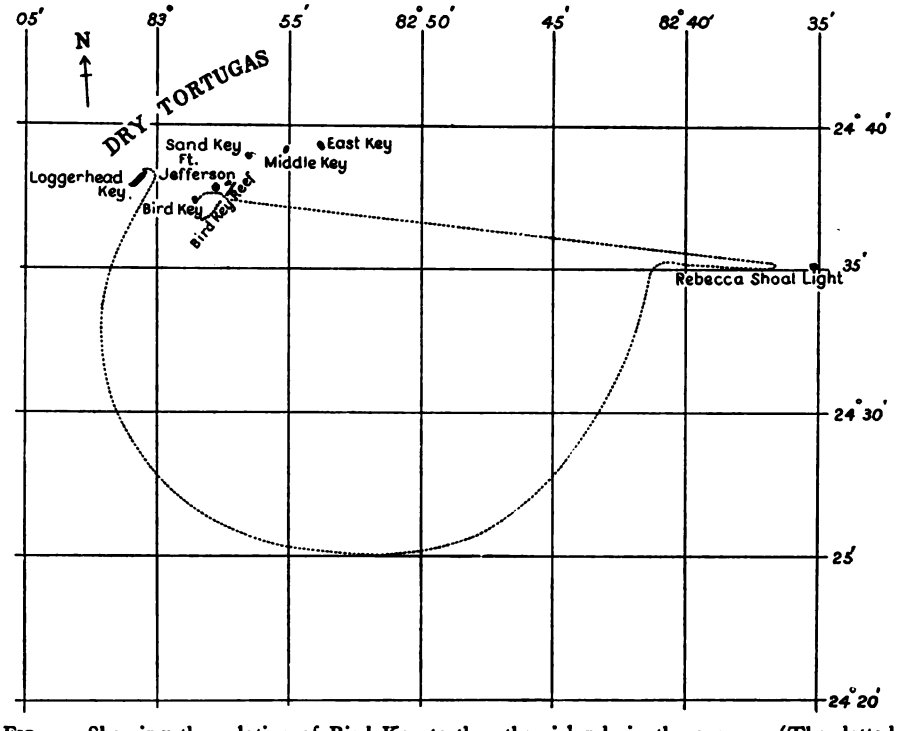

FIG. 1.—Showing the relation of Bird Key to the other islands in the group. (The dotted lines show a launch trip made to determine the feeding habits of the birds.)

(1907) only one severe storm visited the island, and this was not very destructive to the life of the birds.

Owing to its juxta-tropical location, its slight elevation, and the condition of its surface (largely coral sand), the actual surface-temperature of this island is very high, ranging at times during the hottest days from 124° to 143° F.

With the exception of the bay-cedar bushes, which are very abundant upon the central and western parts of this island, little vegetation exists. On a certain limited portion of its surface (southeastern) a dense growth of cactus is to be found. Both cactus and bay-cedars are utilized by the noddies for nesting-places.

No accurate data exist concerning the number of years these two species have migrated to this island for the purpose of rearing their young. The oldest inhabitants of the neighborhood say that as long as they can remember

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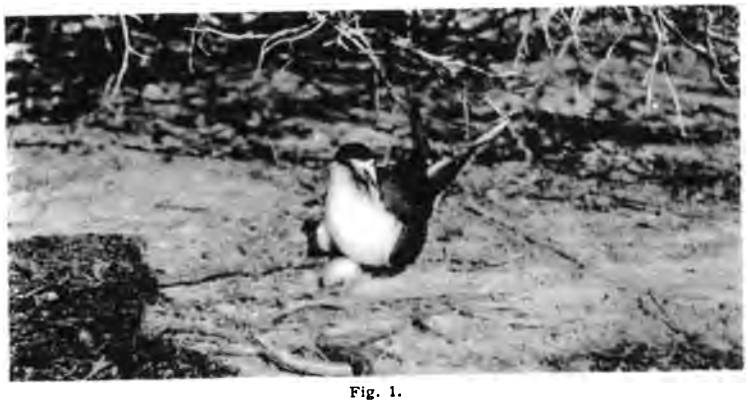

Fig. 1.

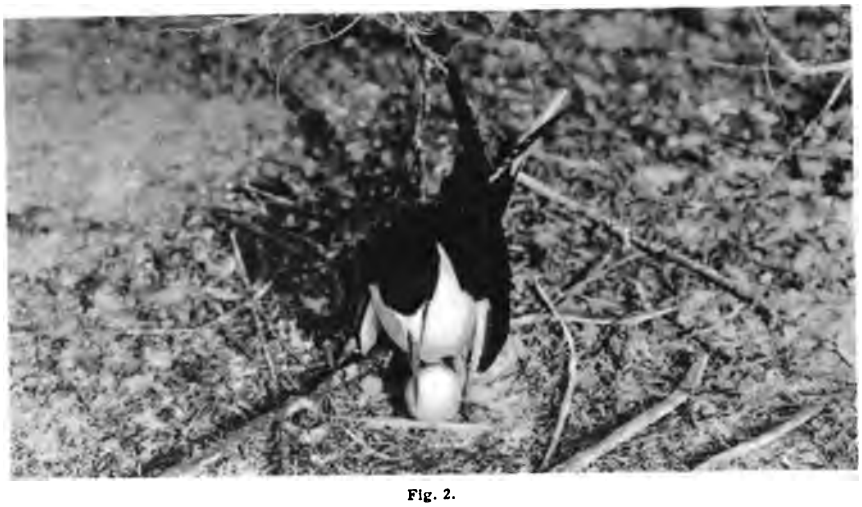

Fig. 2.

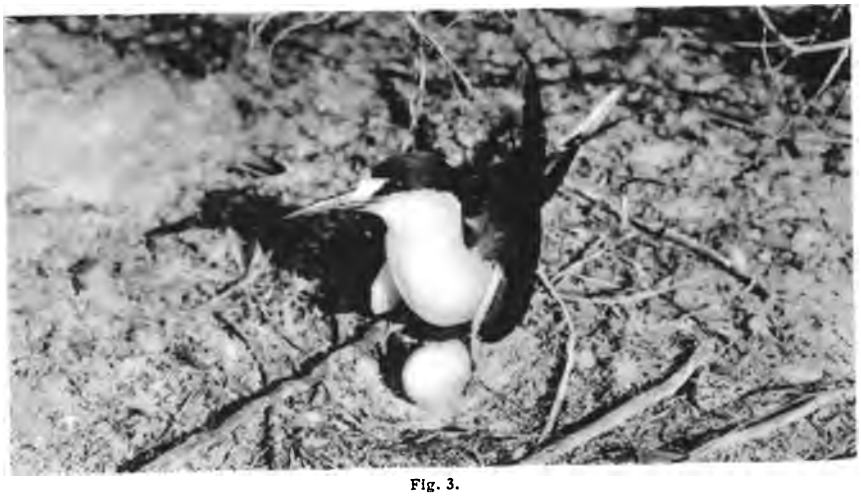

Fig. 3.

Nesting attitudes of Sooties.

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the birds have been going there year after year. The terns arrive at approximately the same time each year (during the last week in April), live there until toward the first of September, and then begin their southern migration.

FOOD AND FEEDING HABITS OF THE TERNS.

In a locality where marine forms are so abundant as in this favored Gulf region, the terns collect their food with little difficulty. They feed upon small fish of different kinds, which are present in great abundance.[1] I have searched in the literature for statements concerning the methods utilized by these terns in catching their fish, but I was nowhere able to find any statements of value concerning this. I made a careful study of the water habits of these birds. To my great surprise, I found that the birds never swim nor dive. As a matter of fact, they never touch the water except when drinking or bathing. The bird drinks the sea-water as it skims the surface of the water with open beak. Bathing they perform in much the same way, never coming to a stop in the water nor completely immersing the body; usually the breast and head are the only parts dipped into the water.

The birds fish by following schools of minnows which are being attacked by larger fish. The minnow, in its efforts to escape, jumps out of the water and skims the surface for a short distance. The terns pick off these minnows as they hop up above and over the surface of the water. The rapidity and accuracy of visual-motor adjustment in this reaction is wonderful.

The birds feed singly or in groups, usually in groups. The group may be composed of both noddies and sooties and may contain sometimes as many as 50 to 100 individuals. All during the day groups of noddies and sooties may be seen at work. As the minnows cease to jump above the surface of the water, the group disbands and scatters in every direction. An instant later, as an attack is made upon the minnows in some other locality, the birds immediately rush there and renew their feeding. Whether there is a true following instinct at hand in this reaction can not be stated, but when one considers that such an instinct is probably present in the sunning reaction (which will be described presently) one feels justified in assuming that the act of feeding in groups is likewise a sign of gregariousness.

In view of my experiments upon the function of distant orientation in these birds, it became very necessary to ascertain when the birds leave the island, how far they go, and when they return. Taking up these questions in order, I suggest the following probable answers: Both species of birds leave the island at early daybreak. In order to observe this more accurately, I rowed out from the island at 3 o'clock in the morning to a distance of 1.5 knots. No birds were seen on their way to feed until daylight began to appear. From that time they appeared in ever-increasing numbers—noddies

[1] Examination of the stomach contents of both young noddies and sooties showed the presence of representatives of the two families of fish Casangidæ and Clupeidæ.

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and sooties leaving the island singly and in small groups. They apparently continue their flight until the jumping schools of small fish meet their eye. This may happen soon or late; consequently they may feed near the island or far away.

Apparently, at the end of 2 hours the noddy has supplied its needs, for at this time it returns to the island and relieves its mate at the nest. The latter then comes out upon the water and takes, roughly, a two-hour turn at fishing, then likewise returns to the nest. This routine of spending 2 hours at the nest and 2 hours on the water is engaged in by all of the noddies during the seasons of brooding and of rearing the young (see p. 206). Before the egg is laid, however, the male does the fishing for both himself and the female at intervals which I could not determine. The male sooty, on the other hand, as will be shown later, during the laying and brooding season probably stays out upon the water all day long, returning at nightfall during the former season to feed the female, and during the latter season to take his turn at brooding the egg (see p. 209).

I was especially anxious to determine the distance to which the terns go for their food. I have the following observations to report bearing upon this subject: So far as I could learn from questioning the residents at Key West, 65.8 statute miles to the east, these birds never venture as far as that for food. The lighthouse-keeper at Rebecca Shoal Light,[1] 17 knots distant from Bird Key (east), tells me that he has never seen either of these species of birds fishing in that locality. He reports that on sunny days pelicans, frigate-birds, cormorants, boobies, etc., appear there in large numbers. I am inclined to think that his statements with respect to the terns are correct. Both on approaching Bird Key from the east and upon leaving it to the west, I was not able to observe these birds feeding farther out that 4 to 10 knots. As a final test in the matter I made a trip, with the assistance of Mr. Kellner and Mr. Hooker, in the laboratory launch. The chart is shown by the dotted lines in figure 1. We left Bird Key at 8^h 30^m in the morning and journeyed in a straight line almost to Rebecca Shoal Light. The birds were seen fishing in numbers until a distance of 9 or 10 knots had been traversed, after which fewer and fewer birds were sighted. From 13 knots on to 15 no birds were sighted. At this point we stopped and waited for an hour. No birds appeared. In returning to the island, we partially retraced our path and then turned toward the south and steered in a circle, keeping Bird Key within about 10 knots. On the return trip, 20 birds were counted before we began to circle the island. Just as the turn was made to the south, three large groups were seen feeding, and from that point on the birds were numerous.

From my own observations I conclude that these birds rarely leave the

[1] See fig. 1, p. 192.

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island for distances greater than 15 knots. Further observations are sadly needed at this point, specially with reference as to whether the birds may not possibly journey further in other directions than in the easterly one. Also as to whether the birds have to go further during stormy weather in order to obtain their food. At all of the above distances, the lighthouse on Loggerhead Key, 160 feet in height, could be "sighted" by the birds at the elevation at which they fly.

From other observations, too numerous to mention separately, I conclude that all birds return to the island at night. Many times just at sundown I have come from Loggerhead Key to Bird Key. The terns are coming in by hundreds and thousands, flying low over the water. By the time twilight has faded the water is entirely deserted. Several trips made to Fort Jefferson late at night showed that these birds do not leave the island at night. The moment the island is reached, however, no matter at what hour of the night, one finds the sooties busily flying from one place to another on it.

While I made these observations as carefully as I could, I realize that conclusive deductions can not be made until a more extended study has been undertaken.

THE MATING OF THE NODDIES AND OF THE SOOTIES.

According to Thompson,[1] both species mate before reaching the island. Whether or not this statement is true can not be answered from my own observation. I did not begin my work upon the birds until May 4. Since they reached the island upon April 29, I could not observe their early behavior. But as I arrived only 5 days later than the birds[2] and found both species actively engaged in nest-building and some beginning to lay,[3] it seems quite clear that mating is either a very simple process, requiring little time, or else it had been accomplished before or during migration. A complete account of mating can scarcely be given until we know more of the life of these birds before their northern migration begins: Are they gregarious previous to it; if so, to what extent? Are the partnerships formed during the mating season kept after the young are reared? What are their habits in feeding and in roosting, etc.? Do their habits change at the approach of the time for migration? What is the length of time for migration? What are their habits during migration (*i. e.*, do they stop on land at intermediate points), etc.?

My notes contain a rather full account of a striking series of reactions between two noddies, which I took to be a case of mating and choice of

[1] *Op. cit.*, p. 78.

[2] I am quite sure that I reached the island before many of the birds. Apparently the birds, the sooties at least, arrive in groups stretching over a period of about two weeks.

[3] Two noddy eggs were found May 4, while the sooty eggs were first found on May 7.

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nest-site, but since it occurred late in the season and did not lead to a completed nest I advance it tentatively:

One day I observed several noddies "sunning" upon the wire covering of one of my large experimental cages. Suddenly, one of the birds (male) began nodding[1] and bowing to a bird standing near (female). The female gave immediate attention and began efforts to extract fish from the throat of the male. The male would first make efforts to disgorge, then put the tip of the beak almost to the ground and incline it to the angle most suitable to admit her beak. She would then thrust her beak into his (the ordinary feeding reaction). The feeding reaction was alternated with the nodding. After this series of acts had been repeated 20 times, the male flew off and brought a stick. He deposited this near the female and then again offered to feed her. She again tried to feed, then the male attempted sexual relations. She immediately flew away, but almost immediately returned and alighted at a slightly different place. The male again brought the stick and again bowed and offered to feed her. She accepted the food, but again flew away when the male attempted to mount her. At this juncture the island was disturbed and my observations could not continue.

If the above is a genuine case of mating, the process is very simple. It consists in the female's accepting food from the male and engaging in sexual relations with him at a given nest locality. Such a process might well take place *en masse* during the first few hours after the birds alight on the island. I was not fortunate enough to obtain a corresponding set of observations of even this unsatisfactory kind upon the mating of the sooties.

THE CHOICE OF THE NEST-SITE, AND THE MATERIAL USED IN CONSTRUCTION OF THE NEST.

THE NEST OF THE NODDY.

The noddy constructs its nest from (1) loose dead branches of the bay-cedar bushes; (2) of seaweed; (3) of a combination of these; (4) of a combination of either or both of these with various kinds of sea-shells and coral. When the shells and coral are employed, they are often placed as an inner lining to the nest and the egg is deposited directly upon them. The nest itself is a quite variable structure, and usually loosely put together. It is very shallow, and this is rather singular, since the wind often blows the egg or the young to the ground (see figs. 4, 5, 6, and 7, plate 2).

The nests remaining from year to year are utilized by the birds at successive nesting periods; whether or not by the same pair can not with cer-

[1] This nodding reaction is one of the most interesting and ludicrous acts of the noddy tern. It is quite elaborate. Two birds will face each other, one will then bow the head almost to the ground, raise it quickly almost to a vertical position, and then quickly lower it. He will repeat this over and over again with great rapidity. The other bird goes through a similar pantomime. If a stranger bird alights near a group, he salutes those nearest, and is in turn saluted by them. During the pantomime a sound is rarely made.

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tainty be answered at present.[1] On account of this utilization of the old nest from year to year, some of the oldest nests have grown to enormous size, due to the addition of new materials at each successive season.

The photograph of the group of nesting noddies (fig. 22, plate 8) shows the tallest of the bay-cedars (about 12 feet) and what I judge to be some of the oldest nests. Figure 5, plate 2, shows a newly constructed nest, which is much smaller.

The statement has been made that the noddy sometimes lays its eggs directly upon the ground, but this is not quite true for noddies on Bird Key.[2] Very often the nest has the appearance of being constructed directly upon the ground, but a closer examination usually shows that it has been built upon a tuft of grass or upon the stem of a bush, the branches of which have been broken off close to the ground. Figure 22, plate 8, shows the characteristic groupings of the nests. It is typical of many localities on the island. Attention is called to the fact that the height of the nests above the surface is quite variable. The noddies apparently do not seek to nest in the thickest parts of the bushes. Although isolated nests are present even where the shrubs are most dense, by far the majority of them are to be found in bushes which border upon open spaces. When we consider the size and delicacy of their wings this fact has biological value in that nests in such situations are easy of access. Apparently there is no instinctive tendency to secrete the nest. The cactus growth contains about 20 per cent of the total number of nests. The nests there do not differ in construction from those found in the bay-cedar bushes.

By means of a mechanical counting device it was found possible actually to count the total number of (active) noddy nests. The count gave 603 nests. In some places, where the bay-cedar bushes are very dense and the area has to be covered "dog fashion" (or at times even still more primitively), and in others where the cactus growth is very luxuriant, error in counting was easily possible. On account of these possibilities of error, I believe that 700 nests is a more representative number. Since 2 birds occupy one nest, we have a total of 1,400 adult noddies on the island.

THE NEST OF THE SOOTY.

The nest of a sooty, when a nest is made, consists of a shallow oval depression in the sand. This depression varies greatly in depth, depending

[1] A test designed to answer this question was made. Before leaving the island, I caught three birds on three separate nests. I marked the nests and placed a platinum band around the legs of the birds. During the nesting season, just past (1908), Dr. Mayer wrote me that he had captured the birds occupying these marked nests and *that none of the birds so captured was marked with the platinum band.* It is recognized that the number of birds tested in this way is too small to afford a basis for generalization.

[2] The nearest approach I found to the laying of the egg upon the bare ground was in the case of two nests built on a bare horizontal board lying among the cactus growth. In each of these cases the egg was laid directly upon the board, but some dozen or two small sticks retained the egg in position.

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upon the nature of the surface. It is rarely over 5 cm. in depth, even in loose sand.

The northern and northeastern sections of the island are free from bushes, but are covered by a shallow growth of Bermuda grass. These areas contain by far the largest number of nests. The group photographs of the sooties appended (see especially figure 17, plate 6) are taken at one or the other of these sections. The eggs in these areas are laid literally on the grass and bare earth in no kind of nest structure. The eggs are often deposited in open sandy places, but nest depressions are not always made, even where the nature of the surface easily permits it. A reference to figure 18, plate 6, will show quite clearly the absence of any complex nest-structure.

A rather interesting variation in nest-structure appears among certain nests which are built under the bay-cedar bushes. The leaves from the bushes sometimes form a carpet over the sand. The nesting sooties often gather up these leaves and place them around the rim of the depression. Under no circumstances are the leaves collected from a distance further than the birds can reach with their beaks while remaining in a sitting posture in the nest.

The nests of the sooties are assembled into groups. Roughly speaking, there is a southeastern, a central, a northern, and a northeastern group.

An approximate count of the total number of the sooty nests was made in the following way: Those parts of the surface of the island containing nests were subdivided into ten separate areas. The number of square feet in each area was next determined. The average number of nests (spots where eggs were deposited) per square foot was then determined separately for each area. By means of these data, the total (approximate) number of nests on the island was found to be 9,429. Multiplying by two, as in the previous case, we have 18,858 as the total number of adult sooties. It may be said that the above determination was made late in the brooding season, after all the eggs had been laid. It may also be of interest to note that in localities where the nests are very numerous they often are not more than 10 to 12 inches apart. On account of this close grouping of the nests, and of the quarrelsome nature of the brooding birds, *exact localization of nest* and *recognition of nest and mate* easily became the most important features in the lives of the sooty terns. This situation affords a convenient starting-point for a psychological study of the behavior of these birds. My tentative beginnings in this field are described on pages 221 ff.

REACTIONS OF THE NODDIES OBSERVED IN NEST-BUILDING.

My notes, written during the observations, contain a large amount of material relating to the way in which the noddy and sooty nests are constructed. The greatest difficulty in obtaining accurate notes lies in the fact that in neither of these two species are the differences in visual appearance

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between the male and the female marked enough to afford a basis for determining sex. But with close observation, the differences in behavior are so marked, at least during the nest-building and egg-laying stages of the nesting period, that the following statements, which refer to the division of labor between the two sexes, are fairly accurate. Later on in the work, I found that observation was greatly aided by marking one of the birds with oil paint, and then from the behavior of the marked bird record whether it was the male or the female.[1]

On May 11, the following notes were obtained from a pair of noddies at work upon a nest which had been started a few days previous:

Both birds work, bringing sticks, sea-weed, shells, and coral. Both birds shape the nest clumsily by pecking and pulling at the sticks. They never weave the sticks so as to form a compact and durable nest. The stick is dropped on the rim, then drawn into position. Frequently, first one bird, then the other sits in the nest and shapes it. In order to do this the bird rises on its feet and depresses its breast and turns round and round. The material is obtained both far and near. Floating sticks and seaweed are gathered from the water. They frequently alight under the nests of other birds and gather up the fallen branches. They even take the material from other nests which are left momentarily unguarded. Frequent fights ensue. The birds work neither steadily nor rapidly; 10, 15, 20 minutes may elapse before either makes a trip.

On one of the trips the male grasped a large, dead branch which was fast. Another bird came up and also grasped the stick. A fight ensued in which the intruder was worsted. The male next picked up a large stick and attempted to walk out into an open space in order to rise. An obstruction barred the way. The bird, standing on the outside of the barrier, tugged and tugged at the stick, but unavailingly. Finally he stooped under the obstruction, grasped the stick and backed out. This observation is of interest in that it shows a rather wide range of instinctive adaptations. Both birds are busily engaged for the next hour. Then the male leaves, while the female remains sitting on a limb near the nest. Two hours later the male returns and *feeds* the female.[2]

On another occasion in watching the transfer of material from one nest-site to another it was found that one bird did all the work; the other remained sitting on a nearby branch.

Still another observation was made in which it appeared that the male did most of the work. The observation began just after the male had fed the female. The male flies away (4^h 16^m p. m.), but returns with a fine straw at 4^h 18^m. Leaves and returns with straw at 4^h 19^m. Leaves at 4^h 20^m; returns at 4^h 23^m, bringing no material; sits on nest for a moment and preens feathers. Leaves at 4^h 26^m and at 4^h 27^m returns with another straw. Several straws are then brought at intervals of about one minute. On one trip female is sitting in nest. The male returning with straw forces her out, deposits the straw, and shapes the nest. He leaves and returns with a piece of coral. The female then becomes active and brings a small

[1] Sexual behavior gives the most reliable data.
[2] See p. 202 for details.

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white shell and deposits it in the nest. This she repeats two or three times. Both birds are active from now on until 5^h 05^m, at which time the male leaves for food. At 7^h 05^m he returns and feeds the female.

The remarkable thing in all of these acts was the accuracy of orientation. Many nests intervened between their own and the open spaces and many other nests were in process of construction in the same bush. The nest was localized with great exactness by each of the two birds at every trip.

Finally, it may be said that the nest-building instinct is not so *transitory* as certain others. All during my stay on the island the noddies were carrying sticks; even those caring for young do not resist the impulse to gather up sticks. All my efforts to get control of their reactions by supplying them with food and water were unavailing, but I could easily induce activity in them by collecting a bundle of twigs and tossing them up in the air. Hardly would the sticks fall before the noddies were after them. A noddy in mid-air carrying a stick and dodging a dozen other birds in order to maintain possession of the prize is one of the most common sights on the island. So active and alert are they on the wing that if a stick is by chance dropped while the bird is in flight, it is often caught before it strikes the earth or the water.

REACTIONS OF THE SOOTIES OBSERVED IN NEST-BUILDING.

The building of the sooty nest is quickly accomplished. The obtaining of a nest-site is the difficult part of the reaction. As has been said, the sooties build their nests very near one another. For this reason it is extremely difficult to make complete observations. My observations began late one afternoon, before any eggs had been laid. Hundreds of the birds were grouped together, incessantly fighting and screaming. It quickly became apparent that most of them had chosen a nest-site and were defending it against all late-comers. Both male and female were present. Each pair in this particular locality defended a circular territory, roughly 14 inches to 2 feet in diameter. Other birds in wandering around would stumble into this sacred territory and a fight would ensue. The fights would often lead to encroachments upon the territory of still other birds. The number of those fighting would thus be constantly increased. I have seen as many as 14 sooties thus engaging in a fight. Birds 10 and 15 feet away would rush into the fight and the noise and confusion beggared description. Sometimes as many as 10 or 15 such fighting groups could be observed in the area of 1,000 square feet. Quiet would momentarily ensue and then be broken by another series of fights. During the choice of the nesting-site the fights continue day and night, with only intermittent periods of quiet.

Within this charmed circle the two mated birds remain relatively quiet. At this time sexual activity is at its height. It frequently happened in the sexual process that the two birds would step outside of their own territory

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Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

Nesting attitudes of Noddies.

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and a general fight would ensue. When the sexual reaction is in progress it is a signal for the surrounding males to encroach. Coition is thus completed only after much fighting. I have seen the male attempt to mount the female 12 to 15 times and at each attempt be interfered with by neighboring males.

The actual construction of the nest, when a nest-structure is formed, begins after an undefended area has been found. The process of nest-building is somewhat as follows: The bird puts the breast to the ground, thereby supporting the body and leaving the legs comparatively free. The feet are used as a combined scraper and shovel. A few backward strokes of the feet are made, which serve both to loosen the sand and to remove it from beneath the body. The bird then turns slightly and repeats the process. When it has turned 360° (or less) it begins to use the breast as a shaper. By continuing this process, the depression is soon made to assume the required diameter and depth. My notes show that the bay-cedar leaves are often gathered up and placed around the rim of the nest as the hole is being dug. I can not say which sex does the work, but I believe that both male and female engage in it. As soon as the depression is made, both birds begin to defend it. Naturally, where no nest is made, the nest-site alone is chosen and defended as described above.

If we compare the behavior of the noddy during this period with that of the sooty as described above, we find that the former is quietly building its nest and engaging systematically in a fixed routine of instinctive activities. The contrast in the behavior of the two species is always marked, but never more so than at this period of the nesting season.

THE DAILY RHYTHM OF ACTIVITIES.

ACTIVITIES OF THE NODDY BEFORE THE EGG IS LAID.

While observing the noddies at work upon the nest, it soon became apparent that the daily routine of the female was different from that of the male. From many hundreds of observations it was also evident that the male feeds the female at more or less regular intervals. Incidental mention has already been made of this difference in the activities of the male and female in the previous sections, but a more detailed statement is in order if we are thoroughly to understand the economic conditions obtaining on the island.

After both birds have worked upon the nest for some time, the male leaves and is gone for varying lengths of time, depending upon the ease with which food is obtained. While he is away the female rarely leaves the nest. She sits usually upon a nearby limb and rarely shows signs of activity. It is not unusual to see four or five females thus sitting motionless and stupid for hours at a stretch. Observation at such a time becomes exceedingly trying. Quiet is occasionally broken by the males from other

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nests attempting to establish sexual relations with these temporarily unguarded females. This is in all cases unsuccessful. Disturbance to some extent is also caused by other birds attempting to poach straws. If the day is hot, the female may make frequent trips to the water. The nest is thus left for a time unwatched. The bird quickly returns, however, and resumes watch over it.

The male returns with a full-laden crop. He alights directly upon the nest or near the female. The female at once shows signs of life, and as they approach each other they begin nodding. Then the male invites the female to feed by putting his beak down to a position convenient to her. She gets the food by taking it directly from the mouth of the male, the male disgorging it by successive muscular contractions of the throat and abdomen. The impression one gets from this ludicrous performance is that the bird is choking to death. During the whole of the process of feeding, a soft, nasal, rattling purr is emitted, presumably by the female. This purring sound is an invariable indication that feeding is taking place. It is to be heard on no other occasion.

At times the male upon his return is not so ready to feed the female. The female then strikes the bill of the male sharply with her own. I have seen the female thus strike the male 18 to 24 times before eliciting the proper response from him. On other occasions, the female is reluctant to feed the proper length of time, whereupon the male gently taps the female and puts his beak near her own again and again. The controlling stimuli throughout this reaction seem to be *organic and visual.* We might schematize the principal features of the reactions, as a whole, as follows:

The male fishes until intra-organic pressure of food in the crop reaches a certain intensity. This acts as a stimulus to return (proximate and distant orientation discussed on pages 224 and 227 respectively). The visual stimulus of mate (and nest and nest locality) coupled with the intra-organic stimuli just mentioned, condition the feeding reaction. On the part of the female we have the intra-organic (hunger) stimulus and the visual stimulus induced by the movements of the male. The male disgorges until there is a cessation of the excessive intra-organic pressure, at which time his feeding movements cease and the female may strike his beak in vain. The female in her turn feeds until there is both a cessation of hunger and a normal intra-organic pressure established. If this takes place before the male is ready, he in turn attempts to further stimulate the female by a slight change in behavior (*i. e.*, "coaxing" by tapping the female and putting his beak down near her).

The feeding reaction completed, the birds often sit near each other, nestling and nodding vigorously. This is the time usually chosen for coition, which takes place frequently up to the time the egg is laid. Feeding may occur at any time of the day, but the best time to observe it is at sunset, when the males are returning in numbers.

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At night the two birds usually remain in branches near the nest, but if disturbed, both fly away for a short distance and circle back almost immediately to the nest. In flying at night both the noddy and the sooty break their graceful flight into short, ungraceful, and ill-directed choppy swoops, very similar to the way the night-hawk breaks its flight when flying after dusk.

During the egg-laying period, which is at the same time the nest-building period, we may summarize the chief points in the lives of the noddies by saying (1) that there is common activity in the building of the nest; (2) that the female guards the nest while (3) the male procures food for both. Both birds are quite wild during this period. If the nest is approached they fly away and make no effort to defend it. For this reason it is difficult to capture and to mark the birds. They fly away at night at the first approach of a lantern or torch. Their behavior at this time, in this respect, is quite different from that observed later on during the brooding period.

ACTIVITIES OF THE SOOTY BEFORE THE EGG IS LAID.

I can say little concerning the separate daily activities of the male and female sooties during the corresponding period. My time was centralized around the nests of the noddies for the first two weeks of my stay, and consequently I lost my best opportunity to study this period of the life of the sooties. The birds are so numerous and the confusion so great at this time that detailed and sustained observations of habits are well-nigh impossible. That feeding of the female occurs I am sure, but I am not sure that the female never fishes for herself. I spent several continuous hours, at different times, observing the nests of the sooties, and the only feeding reaction I saw took place late in the afternoon. The details of the feeding process are very similar to those described above for the noddies, except that when feeding between two sooties begins it is the signal for the approach of dozens of other birds, which precipitates many fights. The noise of the colony as a whole is so deafening at all times that it is impossible to say whether a special sound or series of sounds is made while the female is feeding.

During the period before the egg is laid the sooty, like the noddy, will leave the nest if one approaches, and unless one is quite a distance away the bird will not approach the nest locality. It will circle in the air again and again, giving out the shrill nasal alarm cry of "ëäh, ëäh, ëäh." It is the most restless and noisy bird I know, and almost as much so at night as during the day. Sleep apparently is taken during both day and night by dozing momentarily at intervals. How the bird maintains its vigor with no more continuous rest than it takes is a mystery. This peculiarity of the sooty has led to the popular nickname of "wideawake tern."

ACTIVITIES OF THE NODDY AFTER THE EGG IS LAID.

The noddy lays one egg. It may be laid almost as soon as enough straws are placed together to support the egg or it may not be laid until after sev-

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eral weeks of nest-building. It has been mentioned that the noddy never fully completes its nest; but after the egg is laid the gathering of additional nest-material is a sporadic activity.

The first eggs were noticed on May 4. On May 6 I marked 16 nests and visited each twice daily. The first egg was found in these nests on the 11th; not until the 25th did each nest contain its egg. My chart shows that the majority of the eggs were laid from the 11th to the 16th. Fisher[1] has the following to say concerning the appearance of the egg:

> The rather acute ovate egg is a creamy white, sparsely spotted with light gray, burnt umber, and walnut brown. Most of the brown spots are on the larger half, and are sometimes small and at other times quite large (4 to 8 mm. across). One egg has no dark marks, but is scantily spotted and streaked with light Mars-brown. Specimens vary from 58 by 48 to 51 by 35 mm.

After the egg is laid, a marked change appears in the behavior of both the male and the female. The birds will now attack even a human intruder, and their defense of the nest against their own kind becomes even more strict than before.[2] Oftentimes the birds will sit on the egg and allow themselves to be caught, striking viciously all the while with their long, keen, pointed beaks. Individuals vary greatly in this respect. On my daily rounds, as I approached the vicinity of a group of nests, several noddies would usually advance to meet me, striking viciously at my head. Their attacks would continue until I withdrew. Many times I have had my hat knocked off and the blood brought from my scalp by their vicious attacks. This change in the behavior of the noddies, which is so marked and which begins so abruptly, will be spoken of again further on in the paper. It may be said here that the stimulus to the change is to be sought for in the tactual and visual impulses aroused by the egg.

Still another marked change occurs in the habits of the birds: The male no longer feeds the female. Each bird takes equal turns at brooding the egg. My attention was first called to this while I was watching the habits of the birds before the egg was laid. Several nests in the vicinity of the place of observation already contained eggs. At these nests I was never able to observe the feeding of the female by the male. At this period the two birds become practically automata. Their life is taken up in alternately brooding the egg and in feeding. The birds spend little or no time together except at night. The one comes to the nest, the other flies away to feed.

When the returning bird (which I designate *R*) arrives at the nest, the bird on the nest (which I shall designate *O*) may or may not immediately react to it. To take the most rapid case of immediate "relief" at the nest first, we find *R* returning and alighting on the rim of the nest. *R* nods to *O*. *O* nods in return. This continues for a moment, when *O* takes flight. *R* immediately covers the egg.

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[1] *Op. cit.*, p. 783.
[2] See Thompson, *op. cit.*, p. 81.

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Fig. 8.

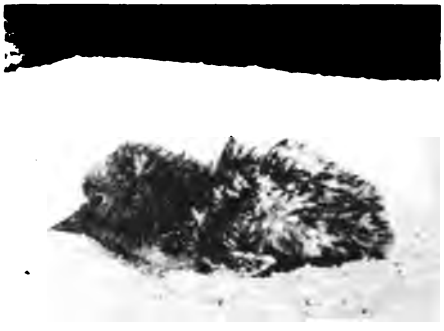

Fig. 9.

Fig. 10.

Fig. 11.

Young Sooties.

Fig. 8. Eight Days. Fig. 9. One Day. Fig. 10. Three Days. Fig. 11. Thirty Days.

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In other cases both *O* and *R* will stay on the nest together for as long as 20 minutes. All the time *R* is "crowding" *O* more and more; suddenly, as *R* receives contact stimulation from the egg, a more pronounced movement is made, thus forcing *O* aside. *O* is thus freed from contact stimulation. *O* gets up, nods to *R*, and flies away. *R* (now *O*) turns the egg with the beak and settles gradually down into the nest.

A few examples are here quoted from my notes:

May 12, 1907. One "relief" noted. *O* had been on egg for a long time. *R* returned and gradually pushed *O* aside. Nodding reaction very much abridged. *O* circled around nest, then flew away.

May 13, 1907. *O* had been on nest 3.5 hours. At 12 o'clock *R* appeared. *R* alighted upon the rim of nest and gave one or two upward flirts with the beak. *O* was then gradually shoved aside. After *O* had been pushed from the egg, both birds occupied the nest together for 15 minutes. *O* then disappeared. In a nearby nest the *R* perched motionless for 25 minutes on the rim of the nest before attempting to push the *O* aside.

The egg is generally covered day and night. Occasional trips are made by *O* to the water for drinking and for wetting the breast feathers. This latter reaction has its value possibly in keeping the egg at the proper temperature. The sun is so hot that if the egg were left uncovered for any great length of time it probably would not incubate. Occasionally, however, *O* will perch for 10 to 15 minutes on a nearby limb, leaving the egg exposed.

After I had observed some 12 to 15 cases of the above interchange of activities at the nest, and found that the average time required for a shift to take place was 2 hours, it occurred to me that the birds might have some mechanism which might function as a time-sense (organic stimulation of some kind, probably). In order to carry out the work carefully, one bird (sex not determined) at each of 3 nests was marked with oil paint (aniline dyes do not resist the action of the salt water). The nests were visited every half hour, beginning at 6 a. m. and continuing until 8 p. m. The observations were continued 2.5 days. In table 1, *M* refers to the presence of the marked bird at the nest, *U* of the unmarked bird. The letter *p* shows the presence of both birds at the nest.

From the table it appears at a glance that the period of occupancy of the nest is a variable one, ranging from 30 minutes to 5 hours. In some cases, however, the sequence is somewhat regular (see May 22, 1907, nest No. 3, from 8 a. m. to 8 p. m). It must be remembered that *R* is the bird which controls the length of time *O* occupies the nest. *O* remains until *R* returns.[1]

It would be interesting to determine the stimulus which leads *R* to return to the nest. *R* does not always appear at the nest the moment the island

[1] Experiments on distant orientation where one bird is removed from the nest for several days at a time show that *O* will remain on the nest without going for food for 24 to 48 hours, but not longer. After this period elapses, *O* will go for food, leaving the nest and egg unguarded.

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TABLE I.—*Various "shifts" made at the nests of the noddies, May 21, 22, and 23, 1907.*

Time.	Nest I.			Nest II.			Nest III.		
	May 21.	May 22.	May 23.	May 21.	May 22.	May 23.	May 21.	May 22.	May 23
6h 00m a. m.	M	M	M	M	Up	U	U	U	M
6 30	M	M	U	M	M	M	U	Mp	M
7 00	M	M	M	M	U	U	U	Up	U
7 30	M	M	M	M	U	U	U	M	U
8 00	M	Up	M	M	U	U	Up	Up	U
8 30	M	U	M	M	M	M	M	U	U
9 00	M	M	M	M	M	M	M	U	U
9 30	M	U	M	M	M	M	M	U	U
10 00	U	U	M	Up	Mp	M	M	M	U
10 30	U	U	U	M	M	M	M	M	U
11 00	Up	U	...	U	M	...	M	M	M
11 30	M	M	...	M	M	...	M	M	...
12 00 m.	M	M	...	M	U	...	M	M	...
12 30 p. m.	M	M	...	M	U	...	M	M	...
1 00	Up	U	...	Mp	U	...	M	U	...
1 30	U	U	...	Mp	U	...	U	U	...
2 00	U	U	...	Up	U	...	U	U	...
2 30	M	U	...	U	Mp	...	U	U	...
3 00	M	U	...	U	U	...	U	M	...
3 30	U	U	...	M	U	...	M	M	...
4 00	U	Up	...	M	M	...	M	M	...
4 30	U	M	...	M	M	...	M	M	...
5 00	U	M	...	M	M	...	M	M	...
5 30	U	M	...	M	M	...	U	U	...
6 00	U	U	...	M	M	..	U	U	...
6 30	U	U	...	M	M	...	U	U	...
7 00	U	U	...	M	M	...	U	U	...
7 30	U	U	...	M	M	...	U	U	...
8 00	U	U	...	M	U	...	M	M	...

is reached. *R* often joins a group of other noddies sunning upon the beach or house-top (preferably the beach) and goes from this place to relieve *O*. We shall here describe the "sunning reaction" a little more in detail.

In the brooding period, this "sunning reaction" (mentioned by Thompson, Palmer, *et al.*) is engaged in largely (1) by *R*'s before they return to the nest; (2) by *O*'s just leaving the nest, and (3) by birds which, I believe, are not attached to any nest. Figures 27 and 28, plate 11, show the noddies collected near the beach. The house-top, the dock and an old wreck, the top of my experimental cages, etc., were all utilized by the birds for this purpose. Although the reaction is at bottom gregarious (similar to the feeding reaction) the birds are stolidly indifferent to one another's presence. They sit silent, head to the wind, elaborately preening their feathers, pecking first at one toe, then at another. Occasionally when another noddy joins the group a mutual nodding is engaged in which at times for no observable reason ends in a fight. The birds here as elsewhere are silent. It is interesting to note that a definite distance is maintained between birds engaged in this activity. The distance is determined, I believe, by the long diameter of the body of the bird—they must have a free space in which to turn. I have seen 10 to 12 birds upon the comb of the roof of the house separated

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from one another by distances so regular that the unaided eye can with difficulty distinguish inequalities in the spacing.

The above reaction was discussed in this connection because of its bearing upon the question of the presence of an "organic time-sense" in the noddy. The birds (*R*'s) often leave these chosen spots to go to the nest and relieve the mate. The probable conclusion to be drawn is that organic impulses furnish the stimulus leading to the return to the nest. If this be the case, we should expect the functioning of such a time-sense to be as inaccurate as our chart actually shows the case to be.

Summing up this long section on the behavior of the brooding noddies, we find: (1) that the presence of the egg brings about a change in the distribution of labor between the sexes; (2) the male no longer feeds the female, but each sex separately obtains its food; (3) the egg is brooded constantly day and night by both sexes, the male and female relieving each other at intervals varying from 30 minutes to 5 hours, the average interval being in the neighborhood of 2 hours;[1] (4) the most significant general reaction caused by the presence of the egg is the change in the disposition of the birds. Before the egg appears, the birds are shy and leave the nest at the slightest disturbance; after the egg is laid, the birds will defend the nest against even human invaders.

It is a little hard for the student absorbed in mammalian behavior alone to understand the fixed character of all these responses—the relative lack of any large store of latent adaptability and plasticity. These reactions preserve the birds and have preserved them for ages in this favored environment. There is no need for a larger repertoire of reactions. There is good material here for the study of the acquisition of habits and the permanency of such habits in an organism which is by nature already so largely adapted to its environment.

ACTIVITIES BY THE SOOTY AFTER THE EGG IS LAID.

The sooty, like the noddy, as a rule lays one egg, although I counted some 25 cases where a nest contained 2 eggs and, in one observed case, 2 birds were actually hatched and reared. The first egg was laid on May 7. By May 15 thousands of eggs were present. Fisher[2] has the following to say concerning the markings of the sooty egg:

> The ground-color is white or occasionally a cream buff. One type of marking consists of deep burnt sienna and grayish vinaceous spots, with occasional nearly black scrawls scattered rather evenly over the whole surface. These spots are 1, 2, and 3 mm. in diameter, with occasional larger and smaller ones. Another less prevalent variation consists of heavy, very deep burnt sienna blotches (5 to 15 mm. in

[1] It would be interesting to determine whether the birds relieve each other at night, or brood the egg on alternate nights, or finally, whether one sex always retains possession of the nest at night.

[2] *Op. cit.*, p. 780.

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extent) congregated in a zone near the blunt end, and lesser pale grayish vinaceous and deep burnt sienna spots sparsely scattered over the rest of the egg.

The general disposition of the sooty, like that of the noddy, changes after the egg is laid and in the same way. Some of them become far bolder than the noddies in a corresponding situation. It was possible for me to lie down within a few inches of a brooding sooty and have it remain on the nest indefinitely. If the hand is extended toward the sooty it will attack vigorously, but I have never had a group of flying sooties attack me as I approached the vicinity of their nests, as was sometimes the case when I ventured too near the nests of the noddies. The birds are very variable in this respect. When one approaches a neighborhood containing many nests, the majority of the birds will fly up into the air, circling round and round, screaming all the while. If one remains quiet, the birds will gradually return and cover the eggs. Gradually the nests nearest one's position will be cautiously approached and then occupied. A certain small percentage of the birds will remain on the nest, no matter how violent the disturbance.

My study of the instinctive reactions of the brooding sooties was again beset with difficulties because of the large number of birds present. My method of studying their behavior was similar to the one just described for the noddies. I would choose a favorable spot where several nests containing marked birds could easily be observed at once, then record what went on at each separate nest. I speedily found that the nesting reactions of the brooding sooties are quite different from those of the noddy. I would sometimes spend 4 to 6 hours at the nests without seeing a single bird leave its nest except to make short excursions for the purpose of fighting or to obtain water. The following day would sometimes find the same bird on the nest, sometimes its mate. In order more accurately to obtain data upon the question of the division of labor between the two sexes, I made a table (table 2) similar to the one presented for the noddies. At first the observations were taken every half hour, but as soon as it became apparent that so many observations were needless the period was lengthened.

It appears conclusively from table 2 that the shift at the nest is roughly a diurnal one, but that at times it may not occur except once in 48 hours. All of the factors in this reaction do not appear in the table. Apparently most of the shifts are made at night. I attempted on many occasions to determine the hour of shifting by leaving a lantern near the nest and making observations during the night, but the light could not be arranged so as not to frighten the birds, and their reactions consequently were not natural. The birds would refuse to cover their eggs if the light were made intense enough to be of value to me.

Then again, in certain cases, the shift is not made within the 24-hour period. Where is the absent bird? All my efforts to discover its presence near the nest failed. Does it go such a great distance for food that it must

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Fig. 12.

Fig. 13.

Fig. 14.

Young Noddies.

Fig. 12. One Day. Fig. 13. Three Days. Fig. 14. Three Days (born white).

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TABLE 2.—*Various "shifts" made at the nests of the sooties.*

Date.	Time.	Nest I.	Nest II.	Nest III.	Nest IV.	Nest V.	Nest VI.
May 21, 1907—	6h 00m a. m.	U	M	M	U	U	...
	6 30	U	M	M	U	U	...
	7 00	U	M	M	U	U	...
	7 30	U	M	M	U	U	...
	8 00	U	M	M	U	U	...
	8 30	U	M	M	U	U	...
	9 00	U	M	M	U	U	...
	9 30	U	M	M	U	U	...
	10 00	U	M	M	U	U	...
	10 30	U	M	M	U	U	...
	11 00	U	M	M	U	U	...
	11 30	U	M	M	U	U	...
	12 00 m.	U	M	M	U	U	...
	12 30 p. m.	U	M	M	U	U	...
	1 00	U	M	M	U	U	...
	1 30	U	M	M	U	U	...
	2 00	U	M	M	U	U	...
	2 30	U	M	M	U	U	...
	3 00	U	M	M	U	U	...
	3 30	U	M	M	M	U	...
	4 00	U	M	M	M	U	...
	4 30	U	M	M	M	U	...
	5 00	U	M	M	M p	U	...
	5 30	U	M	M	M	U	...
	6 00	U	M	M	M	U	...
	6 30	U	M	M p	M	U	...
	7 00	U	M p	M p	M	U	...
	7 30	U	M p	M p	M	U	...
May 22, 1907—	6 00 a. m.	M	U	U	M	M	U
	7 00	M	U	U	M	M	U
	8 00	M	U	U	M	M	U
	9 00	M	U	U	M	M	U
	10 00	M	U	U	M	M	U
	11 00	M	U	U	M	M	U
	12 00 m.	M	U	U	M	M	U
	1 00 p. m.	M	U	U	M	M	U
	2 00	M	U	U	M	M	U
	3 00	M	U	U	M	M	U
	4 00	M	U	U	M	M	M
	5 00	M	U	U	M	M	M
	6 00	M	U	U	M	M	M
	7 00	M	U	U	M	M	M
	8 00	M	U	U	M	M	M
May 23, 1907—	6 00 a. m.	U	M	M	M	U	M
	7 00	U	M	M	M	U	M
	8 00	U	M	M	M	U	M
	9 00	U	M	M	M	U	M
	10 00	U	M	M	M	U	M
	11 00	U	M	M	M	U	M
	3 00 p. m.	U	M	M	M	U	M
	5 30	U	M	M	M	U	M
	7 15	U	M	U	M	U	M
May 24, 1907—	7 30 a. m.	M	U	U	U	M	M
	9 00	M	U	U	U	M	M
	10 00	M	U	U	U	M	M
	3 00 p. m.	M	U	U	U	M	M
	5 00	M	U	U	U	M	M
	7 00	M	U	U	U	M	M
May 25, 1907—	8 00 a. m.	U	M	U	U	U	M
	12 00 m.	U	M	U	U	U	M
	8 00 p. m.	U	M	U	U	U	M
May 26, 1907—	8 00 a. m.	U	M	U	M	M	U
	7 00 p. m.	U	M	M	U	M	U
May 27, 1907—	7 00 a. m.	M	U	U	U	U	U

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remain away over night? The nearest land (and the birds never swim nor rest on the water) is 45 miles away (Marquesas, a very small key), and there is no evidence, so far as I know, that these birds visit there (none remains over night on the small islands belonging to the Tortugas group). On page 194 it is shown that in all probability these birds do not leave the island for distances greater than 15 knots in their search for food, and that they return at nightfall (or shortly thereafter) and leave at daybreak. My explanation of this failure to "shift the watch" is found in the peculiar restless nature of the birds. In actually observing their behavior during the shifts which occurred toward nightfall, I found that *R* would come and push *O* aside. *O* would leave for a few moments, then would return and scrouge back upon the nest. This would sometimes be repeated three or four times, one bird leaving the other temporarily in possession of the nest. If this procedure were gone through with in the early morning hours, it is easy to see how the wrong bird might easily join a group of other sooties leaving the island for food. *O* would thus be left in possession of the nest for two days in succession. The settlement of this point is one extremely to be desired. If later controlled experimentation is ever to be undertaken, it is necessary for us thoroughly to understand their feeding and nesting habits.[1]

Occasionally my records show the presence of both birds at the nest for several hours at a time. The general behavior of the brooding birds can best be understood by citations from my notes, which were made at the time and place of observation. By the following citations I hope to give a general impression of the behavior of the sooty colony at a time when its life is most complex, about the middle of May. Some of the birds have laid and are brooding their eggs, while others have not yet laid, but are present defending the nest-sites. In order to facilitate description, I shall use the letter *S* to designate the bird brooding the egg (the "sitter") and *G* to designate the mate of this bird, which is usually standing guard (when present). The term "layers" is used to designate those birds which have chosen a nest-site but have not yet laid the (one) egg. Reference to the habits of the latter should more properly have been made on page 203, but since the behavior of the "layers" influences the behavior of the brooding birds to some extent they enter into the observation.

May 13, 1907. Position taken near large group of "layers" and "sitters." The *S*'s droop their wings and waddle around the egg, finally sitting down upon it in a stiff and clumsy fashion. They are very much more restless than the noddies. They are constantly engaging in fights, leaving the eggs in order to do so. They turn round and round frequently, orienting the head differently at each adjustment. In some cases the *G* is present. In one

[1] It is suggested that the nesting behavior at night could be studied by means of flashlight photographs if the birds and nests were prominently enough marked. Fig. 21, plate 7, shows poorly the possibilities in this method.

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case it stands about 2 feet from the nest, fighting all birds which approach. Once when this *G* drove a strange bird too near *S*, *S* left the egg to assist in the fight. Often in sitting down on the egg *S* rocks it gently, turns it with the beak, and gradually brings her weight upon it.[1]

Birds on alighting, if orientation has not been exact, have to run the gauntlet of hundreds of sharp beaks before they finally reach their own nests. Since this is constantly occurring, it greatly adds to the general confusion. Where the nests are under the bay-cedar bushes the birds on returning usually alight near the edge of open spaces and then run on foot to their nests, while if the nests are in the open spaces they circle around until the nest is located, and then alight.

During this observation I saw three cases of feeding at nest-site where no egg had been laid. Feeding was accomplished with great difficulty. Dozens of other birds attempted to interfere, especially the *G*'s of nearby nests.[2]

One case of shift at the nest was observed. *S* had been on the nest during the whole previous time of observation. Suddenly *G* went to the nest and gradually pushed *S* aside. *G* sat on egg for a few moments, then got up. *S* sat down on egg immediately. *G* then returned, pushed *S* aside, adjusted carefully, and remained on the egg.

During this observation and in many others my attention was called to a peculiar reaction in the male. When approaching his mate and at times other females, he would arch his neck, droop his wings, lower his head slightly, turn the head to one side, and strut around and around the female, at times raising his head and then lowering it. The reaction is very similar to the one exhibited by the cock of our common barnyard fowls when he has called the females to feed. Figure 19, plate 7, shows 2 males in this attitude.

My notes show that in some cases during the brooding period the birds sit quietly on the egg the whole day long, even in the midst of the turmoil which is ever present.

In summarizing this unsatisfactory section we may say:

(1) The presence of the egg brings about a change in the disposition of the sooty which is very similar to the one already noted in the noddy.

(2) One important difference between the two species of birds is to be noticed—whereas the shift at the nest in the case of the noddy occurs once in 2 hours, the shift in the case of the sooty occurs once in 24 hours. This leads us to conclude that there must be an enormous difference in the way in which organic data function in controlling the reactions of the two species.

The general impression one gets from close observation of the sooty is that auditory and visual stimuli play a more important rôle in its life than in the life of the noddy.

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[1] See fig. 2, plate 1.

[2] This same reaction was often noticed when the parents attempted to feed the young.

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ACTIVITIES BY THE NODDY AFTER THE EGG IS HATCHED.

The period of incubation varies for the noddy from 32 to 35 days. This fact was determined on the basis of 16 observations. The young began to appear on the island about May 9 (1907). The development of the young of both species is discussed separately further on in this paper. Under the present heading I shall mention only the change that the presence of the young brings in the behavior of the parents. At this period there is an increased tendency to defend the nest. They will now attack with vigor other noddies which approach too near the nest, the sooties and the frigate birds (*Fregata aquila*). From the writings of others I had drawn the conclusion (1) that the frigate-bird attacks the terns and forces them to disgorge, and (2) that it feeds upon their young. I spent many weary hours in attempting to discover the relation of the frigate-bird to the terns, especially its relation to the noddies. Since the noddies build their nests in the bushes where the frigate-birds roost, it was presumed that there if anywhere the devouring tendency of the frigate-bird ought to appear.[1] I found that the cause of the disturbance between noddy and frigate-bird lies chiefly in the fact that the latter, in attempting to find a bush in which to rest, sun, or roost, will oftentimes alight upon or very near to a noddy nest, whereupon the noddy most immediately concerned and those nearby will attack the frigate-bird and at times even rout him. It is a common occur-

[1] When I first went to the island, about 50 frigate-birds were present. The number gradually increased during my stay, until at the end 400 to 500 were present. I caught and forced a number of these birds to disgorge (which they readily do), for the purpose of finding whether or not the remains of young terns or of very small minnows, the food of the terns, could be discovered in the stomach contents. I found that the staple article of diet with them is the flying-fish, which they can easily catch. At times I found fairly large herring and mullet. I also killed 2 of these birds, but found no traces of young terns. In one case the stomach cavity contained no food. This latter observation was interesting in view of the fact that for days during unpleasant weather these birds apparently do not leave the island. This fact made me think at first that possibly the young terns were preyed upon by the frigate-birds in bad weather, but I am convinced that the latter can go without food for long periods of time. On the other hand, it must be confessed that after the young terns appear the number of frigate-birds increases and that all during the day, when the sooties nesting in the open places are feeding their young, the frigate-birds line the bushes bordering upon the nests. At times a frigate-bird will swoop down and fly near the ground. This causes all the sooties to fly up and raise a terrible commotion. This soon subsides, only to be repeated an instant later when another frigate-bird flies to or near the ground. I built an observatory on top of the house and a tent in the midst of the nesting-places, and kept the whole island under close inspection with a field-glass (in this connection I wish to thank the firm of Bausch and Lomb for the use during my entire stay of an excellent stereo-binocular field-glass) in order to determine whether the frigate-bird when it made these movements actually picked up the young or whether it was attempting to pick up food which the parent bird had dropped while feeding the young. My efforts were unsuccessful, so far as showing that the frigate-bird really does violence to the young tern or filches its food. The sooty, in contrast to the noddy, never attacks the frigate-bird.

All that I have read about the ability of these birds to control their movements during flight is true. I have observed them many times in mid-air forcing a victim of their own species to disgorge a fish, which one of the pursuers would catch long before it struck the water.

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Fig. 15.

Fig. 16.

Young Noddies.

Fig. 15. Eighteen Days. Fig. 16. Thirty Days.

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rence, especially late in the afternoon, when the frigate-birds are returning, to see hundreds of such fights. The noddy is always careful to attack the frigate-birds by sudden thrusts (usually made from below), dodging quickly to avoid their fearful and powerful beaks.

The curlew is also an occasional visitant on the island. The appearance of this uncouth bird brings forth fierce attacks from the noddies at this period of their stay. Figure 25, plate 10, shows an attack upon one of these birds.

The parent birds alternately feed the young. The length of the intervals between feedings varies from 2 to 4 hours. The appearance of the young does not alter the feeding relations of the parents, which were found to hold in the table shown above. The interesting additional factor is that now when the birds go out to feed they must bring back a supply for the young bird. The question immediately arises: Does the parent actually catch more fish after the young is hatched, or does it catch the normal supply and share that with the young? If it catches an additional supply, what is the stimulus which leads to a more abundant filling of the crop? If an additional supply of fish is not caught, we should expect (1) either that the birds would feed oftener or (2) that they would become very much emaciated while they are caring for the young. Since my observations show that the birds do become emaciated during the rearing of the young, and that they apparently do not go out to feed any oftener, I am inclined to think that no additional supply of fish is (instinctively) provided for the young. The parents simply disgorge when the appropriate stimulus is at hand, *i. e.*, the sight and contact of the young. Since this process would tend to make the parent birds very hungry (or rather enormously to decrease intra-organic pressure) they probably actually catch more fish on any one trip than they would otherwise.[1] But this larger catch may be due to an emptier stomach and not to any instinctive tendency to provide food for the young.

The apparatus for disgorgement is easily thrown into activity in these birds—very much more so than is the case with the sooties. My appearance at a group of nests in which young were present would call forth many such responses. As has already been mentioned, the noddy stays close by to defend its young. The bird usually sits on the nest and scolds in its peculiar, rasping way. Apparently this vocal effort can be better accomplished after the crop has been relieved of its contents; the bird can also probably fight better. Outside of these two possible reasons, I can offer no additional suggestion as to the biological value of this function when it is exercised in this connection.

At this point, as well as at all others, one finds extreme monotony, fixedness, and lack of variability in the responses.

[1] Since the birds nearly always are supplied with enough fish to disgorge at disturbance I doubt whether "hunger" in the usual sense of the word could under ordinary conditions be attributed to them. Increase or decrease in the intra-organic pressure could function in the same way.

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The young are cared for in the nest until they become strong enough to leave it and live upon the ground. The young birds born in low nests, even at a very early age (20 days and even earlier), clamber from them with alacrity and hide in nearby bushes when danger is imminent. In many cases these young birds can not get back into the nest. Under these circumstances they remain near the nest locality, and the parents on returning first alight on or near the nest and later hop to the ground and feed the young bird. It is interesting to speculate upon the method of recognition between parent and young. There can be no doubt at least of an accurate functional recognition. Since the noddy is always silent when contented, the evidence is good that recognition occurs wholly in terms of vision. Whether recognition of young (or of mate by mate) would take place outside of the nest locality is a problem which ought to be solved.

On account of my early departure from the island (July 18) I can say nothing of the methods by which the parents induce the young to fly, to leave the island and to feed. This period is probably one of great interest. At the time of my departure many of the young noddies were on the ground and were attempting to fly. If I may be allowed to advance statements which lie beyond my actual observation, I should say that the parents are not active at all in "training" the young to fly and to feed.

As the young birds advance in age the parents more and more often engage in the "sunning reaction." My opinion is that the young birds first instinctively collect upon the beach, as soon as their wings will support them. In a short time the instinct to follow the adults leaving from this point to go to food will lead them out over the water. The sight of the jumping fish is a stimulus leading to the movements used in catching the fish. This activity engaged in a few times so perfects the hereditary mechanism that the bird soon becomes independent of the parent in an environment where food is abundant.

In summarizing this section we may say: (1) that the parents alternately feed the young at intervals varying from 1 to 4 hours; (2) that their general conduct is not greatly changed at the time of the appearance of the young, the changes actually observable being an increased tendency to protect the nest and to disgorge on being disturbed.[1]

My own observations naturally contain nothing concerning the behavior of these birds when preparing for southern migration. Thompson[2] writes as follows (concerning both noddies and sooties):

> Towards the end of September the birds begin to leave. They leave in great flocks and at night. The entire exodus consumes, apparently, but two or three days; and some morning the observer will find the island absolutely deserted, save for a few crippled birds that have been injured and are unable to follow their comrades.

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[1] As the young advance in age (20 days and at all later ages) the parent will readily leave the nest when disturbed. The tendency in this respect is to revert to the behavior exhibited during the egg-laying season.

[2] Op. cit., p. 82.

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From the reports of most of the residents, I found that the birds generally leave from toward the middle of August to the first of September. That they leave at night is most improbable, unless "at night" means early morning, at or shortly after daybreak.

ACTIVITIES BY THE SOOTY AFTER THE EGG IS HATCHED.

The period of incubation of the sooty egg is 26 days. This observation is based upon 16 marked nests. The development of the young sooty is deferred to a later place in this paper.

The appearance of the young produces a profound change in the instinctive reactions of the sooty. A general change in the disposition of the bird is also noticeable. During the first three days after the appearance of the young, the sooty is reluctant to leave the young and nest on disturbance. Later, the adults fly away at the slightest disturbance, much as they do during the "laying" season. It is interesting to observe at every disturbance of a nesting-place how quickly the ground will be deserted by both young and old, after the young have reached the age of 3 days. As they leave, the alarm cry is sounded and the commotion spreads to all the nearby nests. When quiet is restored the birds again alight near the nest and gradually approach it. The young birds meantime have run to the bushes, where they remain motionless after sticking their heads into the crotch of some bush or depressing the body against any convenient solid object. The protective coloring of the young sooties is marked. When motionless, as above suggested, they are difficult to find. When the adult returns to the nest, the young birds gradually come from their hiding-places at the peculiar, clucking call of the parent. The parents (after the first few days) recognize their own offspring with ease and accuracy, often going to meet them as they emerge from the bushes. If by chance the wrong young bird is met, it is struck with great force. Naturally this is productive of fights between the adults.

If disturbance occurs before the young birds are 3 days old, they will "sham death" in the nest or advance a few feet from the nest and sham death on the open sand. Lying outstretched upon the ventral surface of the body, with head flat upon the ground, it is with difficulty that one believes that life is present. The slightest contact stimulation will cause the young bird to attempt to get on its feet and struggle away.

From 1 to 6 days is a critical period in the life of the young sooty. Hundreds of them are killed by the adults, and were it not for the "death-shamming instinct" thousands would perish. This tendency on the part of the adult birds, especially of gulls, to kill the young has often been commented upon by nature students, but the phenomenon has not been very well understood. The situation as it exists at the Tortugas colony is, I believe, not difficult of understanding. In the first place, we must consider the

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appearance of the young as being strange to the adult sooty. The advent of young is sudden; their movements, marking, coloration, etc., are striking visual stimuli to the adult—especially to those which *have no young of their own* and which are still brooding the egg. As previously stated, after disturbance the adult returns to the nest first, then the young begin to struggle back from the bushes; and those shamming death in the open become active and crawl back into the nest (these latter are especially liable to be destroyed). In doing so, the young must often pass by areas defended by brooding adults. Each adult begins to attack the small bird for exactly the same reasons that it would attack a persistent sand-crab, or a noddy or another sooty. The young bird by its peculiar cries and movements continues to offer stimulation to the adults, and not until the former reaches its own nest or takes refuge in a motionless attitude and in a partially protected place do the attacks of the adults cease. As the young birds gain in agility (and in experience) they rapidly learn to avoid defended areas and to dart quickly by and under attacking adults. On many occasions I have seen from 4 to 8 adults thus attacking a young tern, chasing it for 10 to 15 feet.

At first the parent does not individually recognize its young, but reacts to it by reason of its presence at the nest.[1] Very early, however, there is mutual recognition between parents and young. The parent will advance toward its own young, even when several feet from the nest, and feed it, often forcing it back to the nest by a cumbersome rolling process. The young approaches the parent and nestles under its body. The parent advances toward the nest, often upsetting the young bird, but at the same time advancing it. Both visual and auditory data are used in the mutual recognition of parent and young. That auditory stimuli are functional can not be doubted. Often I have observed a returning bird give a call a long way off; both the adult and the young answer the call and show changes in their reactions. The parent at the nest will get up from the young and the young will stand up, flap its wings, and leap several times a few inches in the air. A moment later the returning bird will alight and feed the young.

In order to observe the influences of auditory data on nest localization, I watched the areas containing nests many times at night. One evening I

[1] This was determined by exchanging young birds. The exchange is not noticed when the birds are very young, but is noticed after the young is a few days old. My notes are very inaccurate at this point. In one case I took the young at birth from one nest (marked) to rear by hand. Two days later I put a new-born sooty in this nest. The reactions of the adults were very curious. The male first came up to the stranger young and gently struck it; the female came up and the young bird attempted to nestle under her and to feed. Other birds from neighboring nests came up, but were driven off. After this the young was treated in the usual way. There is room for interesting and careful work upon this subject. (Some of the noddy young are born with black juvenile plumage, some with plumage that is almost pure white (see fig. 14, plate 4). Now, if a white bird is exchanged for a black one, or *vice versa*, no disturbance is noticed on the part of the parent, even if there is a difference of 3 or 4 days in the ages of the respective young birds.)

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Fig. 17.

Fig. 18.

Groups of Nesting Sooties.

Fig. 17. The nests are made both in the open and under the Bay Cedar bushes.
Fig. 18. Fights among the Sooties are frequent in the congested nesting localities.

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lay quiet and hidden for 3 hours near a large group of nests which was situated under some very dense bushes. The adult would circle over the area and give a call; it would be answered and random movements would give place to direct. The bird would steer immediately for the source of the call. By peculiar chuckling sounds, which are emitted at this period when mates return, one can be sure that the proper nest has been located. I observed this many times during one evening. After the young were 20 to 30 days old I have heard the young birds answer the call of the parent back and forth a dozen times before the latter actually alighted.

The parents alternately feed the young, but instead of a diurnal period of feeding, such as the parents have before the appearance of the young, the intervals vary anywhere from 4 to 7 hours. My observations are few on this point.

Though the parents feed the young at any hour of the day, feeding can be most easily observed at dusk. It has already been mentioned that the sooties hurry home at nightfall in great numbers. From 4 until 8 p. m. this feeding process keeps the island in commotion. The feeding of the young birds has many interested spectators. While I have never seen the terns from the neighboring nests, which may be observing the process, attempt to rob the young bird, I judge from the actions of the feeding parent that such is occasionally the case. If the parent happens to disgorge more than the young tern can take into its beak and the food is allowed to fall to the ground, it is ludicrous to watch the rapidity with which the parent picks up the food and reswallows it. Oftentimes the mate of the feeding parent is near; its rôle is a purely passive one, except when the "spectators" attempt to approach too near. Its part is then to assist in warding them off.

Neither young nor old is quiet during this period of the nesting season. On the contrary, the noise is practically doubled. In addition to the ordinary sounds made by the adults and the new cries which are added at this time, there is present the high-pitched, insistent "peep-peep" of the young terns. Momentarily the sounds of the adults will cease and the cries of the little ones remind one very strongly of a poultry-yard on a tremendous scale.

A reaction very similar to the "sunning reaction" of the noddies, while present to some extent before the appearance of the young, now shows itself in completed form. As may be judged from the feeding habits of brooding birds, practically only a half of the total number of birds is present on the island during the day, and that half is busied in brooding the eggs. Consequently there is little leisure at this time in the sooty colony. After the appearance of the young, the number of birds present on the island at any one time is much larger. When *R* returns to feed the young, *S* usually leaves the nest, but as in the case of the noddies does not always leave immediately to feed. They collect upon the beach and sun themselves, preening their feathers and standing idly about in a way which is quite similar to

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the noddy. Figures 23 and 24, plate 9, show the birds engaged in sunning. The peculiarity in the reaction is that the birds always choose this one spot (the one shown in the cut) in which to assemble. Occasionally the noddies are to be found in the same spot. Figure 23, plate 9, shows the noddies leaving the beach in advance of the sooties. They "sun" nearer to shore than the sooties. Until we know more of the history of the life of the sooty, it will be difficult to understand the meaning of this reaction.

There is one rather interesting difference between the habits of the noddy and those of the sooty which may be mentioned here: Every stake, buoy, or possible resting-place upon the water is utilized by the noddy. It will sit almost motionless upon any object projecting from the water for long periods of time. This habit of theirs is like that found in the cormorants, boobies, and pelicans which are present in the neighborhood. I have never observed a similar reaction in the sooty. I think the sooty always leaves the island and returns to it without at any time having ceased its flight. This seems rather remarkable when we take into account the fact that the sooty leaves the island in the early morning and oftentimes does not return until toward nightfall.

The sooties often soar round and round, getting higher and higher until lost to sight. They usually join the frigate-birds in this reaction. I am inclined to think that the sooty when sufficiently fed spends a large part of its time in such maneuvers. I have never observed the noddies engage in this reaction.

In a note in the previous section, p. 212, we have already discussed the possible disturbance which the frigate-birds produce in the life of the sooties.

When I left the island, the oldest of the young sooties were about 30 days of age. They were still in their juvenile plumage. From 20 days on, these young birds could be found quite a distance from the nest, but the nest locality still exerted its influence to a marked degree, both upon the parents and upon the young, as shown by the fact that when one of the parents returned from its feeding expedition it always alighted at or near the nest. At the sight or the call from the parent, the young bird would hasten toward the nest to receive food. This ability on the part of the birds to approach within a few feet of a spot which to our eyes had no distinguishing marks, but which had served as a nesting-place, is little short of wonderful.

The care of the young, especially from 20 days on, must be an exhausting process for the parents. They become emaciated and somewhat bedraggled in appearance. This is not to be wondered at when we consider that a healthy young sooty can eat anywhere from 20 to 40 minnows of no insignificant size in a day. It may be of general interest to note that after the first few days the parent always recognizes and feeds its own young and no other, and furthermore, the young tern recognizes its own parents and attempts to feed only from them. Never but once out of many thou-

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sands of observations did I see a young tern begging food from a stranger. The statement has often been made by certain observers that young gulls feed indiscriminately from any adult which happens to be near. Such is certainly not the case among the sooty terns.

In summarizing, we may say:

(1) The presence of the young changes the general disposition of the parents; for the first two or three days after the appearance of the young the parents are more ferocious, but as the young bird gathers strength and can get away from danger, the parents become more wary and leave the nest upon the slightest disturbance. In this latter respect, as is similarly the case with the noddies, they, as it were, tend to revert to the habits formerly exhibited during the laying period.

(2) A tremendous change appears in their feeding habits. During the brooding period the birds apparently are away all day; at the appearance of the young conditions are so changed that the birds relieve each other at the nest at intervals varying from 4 to 7 hours.

(3) The birds have more leisure; they utilize this leisure in collecting upon the beach for sunning.

(4) The birds become exhausted in caring for the young.

PRELIMINARY ATTEMPTS AT CONTROLLING THE REACTIONS OF ADULT BIRDS.

The experimental part of my work centered mainly around the young terns, because I could rear them by hand and could control their reactions through hunger. An experimental study of the adult birds is beset with many difficulties. The previous part of my work shows that until the egg is laid the terns can not be approached closely for experimental purposes. Only a short month was open to me after the egg was laid before the young appeared. After the young appeared, practically all of my time was devoted to them. From the middle of May until the middle of June, however, I had time to try the experiments upon the adult birds which are reported below at some length. I found that a month was too short a time in which to capture and tame adult birds for experimental purposes. In captivity, the birds are wild and restless, but unless they are in captivity they refuse to eat even live fish, even when the fish are placed near the nest. As was shown earlier, in the discussion of the feeding habits of these birds, the natural stimulus to the feeding reaction is the sight of schools of minnows jumping over the surface of the water. I may say in passing, however, that two sooties with broken wings learned to appear at my experimental cages whenever I fed the young terns. These two birds learned to eat both live and motionless fish either from the hand or from a dish. I think it not improbable that, had time permitted, I could have captured the birds and taught them to feed from the hand. Had this been done, hunger could then

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have been used as a stimulus for controlling their reactions. In future work it would be worth while to give this method a thorough test and to compare it with the method described below.

A little experimentation soon convinced me that the method of using the nest locality in place of food was desirable under the circumstances, since the stimulus of the nest locality is almost as potent in its effects upon the reactions of these birds as the stimulus of food on the reactions of other animals. While this method of forcing the bird to overcome difficulties in order to reach the nest may not be so accurate nor so uniform in its stimulating effect as is the case when food is similarly used as a stimulus, it certainly has present in it all the elements of naturalness which even a Wesley Mills could demand. Before giving the results obtained from the use of this method, certain experiments bearing upon the general problem of recognition will be discussed.

TESTS WITH NODDIES AS TO RECOGNITION BETWEEN MATES.

My observations at the nests show that there is present in the noddy a very accurate functional recognition of both nest and mate. It will be remembered that, to our eyes at least, the male and female noddy are indistinguishable. The question then becomes a pertinent one as regards the way in which the female recognizes the male and *vice versa*. Is there recognition between the two birds or is the nest alone recognized and reacted to? From much observation, unsupported however by experimental work, it was forced upon me that the male and female could recognize each other, at least within the nest locality (actually observed recognition of this functional kind took place within a radius of 10 to 12 feet).

A few preliminary unsatisfactory tests of the following kind were made upon this subject: Two birds were caught from marked nests and treated in the following way: The black neck feathers of noddy No. 1 were dyed red with Higgins' ink. The white head and eye-spaces of noddy No. 2 were dyed red in a similar manner.

Noddy No. 1.—Released at 4^h 28^m p. m., 30 feet from nest. Flew to water at once and "dived" six times into the water. Circled back to nest, alighted, and covered egg at once (mate being absent). A few moments later the mate returned, would not alight, circled around the nest several times, then sat down near the nest for a long time; then hopped upon the nest and pecked at the marked bird. Sat behind the marked bird for a long time, then both birds began nodding to each other in a very ludicrous fashion. After 40 minutes the unmarked bird crawled upon the egg, the marked bird taking up a position on the rim and nodding to the unmarked bird. One minute later it again flew to the water and began diving. Two minutes later it returned and alighted near the nest. No further family dissension seemed to be caused by the dye.

Noddy No. 2.—The behavior here was in marked contrast to the above. No. 2 was likewise released 30 feet from the nest. Flew immediately to

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nest and covered egg (mate being absent). Both the noddies and the sooties in the vicinity of this nest were badly frightened by this bird. The mate on returning flew round and round the nest, but would not alight near it. The mate would circle out over the water and then back to the nest. Finally the unmarked bird alighted near the nest and fought off an intruder. The unmarked bird sat near the nest, but made no attempt for a long time to take its turn upon the egg. The marked bird became restless under these circumstances. It would hop up and expose the egg, turning round and round and make signs by nodding the head to the passive mate sitting nearby. The mate made tentative efforts to approach closer to the nest and seemed almost persuaded to take its turn, but the relief was not finally effected until 3 hours had passed.

These two tests as they stand prove nothing definitely. They only suggest that any change in the visual appearance of the birds breaks down the customary and habitual responses which take place between birds attached to a single nest.[1] It occurred to me afterwards that since the noddy has become accustomed to the appearance of the sooty, it would have been a more reliable test had I painted the noddy in the guise of the sooty. The vivid red, if the birds sense color-tone (or even the changed brightness) obviously might have been exciting and might have aroused fear. It is just possible that if I had modified the appearance of the two noddies by painting them with different shades of gray that the change in the visual appearance might not have been noticed by the mates on their return.

TESTS WITH SOOTIES AS TO RECOGNITION BETWEEN MATES.

A similar test was made upon the sooty. Two birds were captured at marked nests, the night before the day upon which the tests were to be made. The white throat, breast, and spaces between the eyes of sooty No. 1 were completely covered with burnt sienna (in oil). Sooty No. 2 was painted as No. 1, but with permanent blue instead of burnt sienna.

Sooty No. 1.—Mate on egg. Marked bird tried to alight. All the sooties nesting in the vicinity flew up, raising a tremendous uproar. The bird alighted within a foot of its nest. Its mate and all the other sooties nearby drove the bird away from the nest vicinity, striking it violently with their beaks. It flew away, but returned in 8 minutes. While in the air it called to the mate (still upon the nest), mate got on feet, answered the call, showing evident signs that the call was recognized. Marked bird again alighted within a foot of nest. Violent commotion was again raised in the colony. Mate struck the marked bird violently with the beak and drove it away. Marked bird tried several other times to alight near the nest, but this was not permitted. Wherever in the whole island this bird tried to alight, commotion was aroused. It then disappeared from the island, after vainly trying for 3 hours to approach the nest. It did not appear again that day in the vicinity of its nest. The following morning, however, the marked bird was calmly brooding the egg.

[1] There is a possibility, too, that the disturbance might have been due partially at least to the olfactory characteristics of the dyes.

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Sooty No. 2.—This bird was carried to a position within 20 feet of its nest and released there. The mate was not present. The marked bird, instead of going directly to the nest and covering the egg, alighted some 10 or 15 feet from it and attempted to walk past other nests in the vicinity. A commotion was immediately raised. The other birds brooding their eggs left them to attack this strange object. This bird ran rapidly out of my sight, being fought at every step, and disappeared for 10 minutes. At the end of that time I saw it approaching its nest. Three feet away from its nest it was halted by a row of hostile beaks. It left again and at the end of half an hour put in an appearance. Again it could not reach its nest. (A rather amusing incident occurred at this point. A noddy in search of a stick alighted near this marked sooty. The noddy is usually utterly oblivious to the presence of the sooty when in search of his precious sticks. Such was not the case in the present instance. He dropped his stick, peered at the sooty, extending his head toward it and craning his neck in a most peculiar and unwonted fashion.) After some 2 hours had passed this bird finally reached its nest and covered the egg. The mate on returning[1] showed evident signs of restlessness and disturbance, but finally took up a standing position near the nest. At my approach some 2 hours later the unmarked bird crawled from the nest and the marked bird crawled on. Evidently the family difference had been satisfactorily arranged.

These tests upon the marked sooties, in so far as they show anything of a satisfactory nature, lead us to believe that a change in the visual appearance of the bird is immediately noticed both by its mate and by the other sooties on the island. The disturbance caused by the appearance of these strangely marked birds was very much more pronounced than was the case with the noddies. Such experiments naturally leave the problem of recognition of mate by mate almost untouched. It is a problem, however, which I believe can be attacked experimentally.

TESTS ON RECOGNITION OF THE EGG.

Since the nest is also accurately localized by both the noddy and the sooty, I desired to test whether the egg, the nest, and the nest locality were all of importance in this reaction. I made tentative efforts to arrive at some conclusion as regards this question.

As a preliminary step I colored the eggs of both the noddy and the sooty and then watched their reactions under the changed conditions. The noddy eggs were colored with vermilion, blue-green, and violet aniline dyes. The birds immediately covered these eggs without the slightest change in their behavior being apparent. Eggs similarly colored with Higgins' black ink produced no disturbance. Hen eggs and sooty eggs and eggs made of magnesium sulphate were likewise accepted without question.

In this connection, an interesting incidental observation was made. A noddy before it lays its egg has habits different from those which char-

[1] Since the bird was released in the morning, I was forced to sit near this nest until the mate returned—about 8 hours later!

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acterize it after the egg is laid (see p. 201). I found that by putting an egg in the nest of such a "laying" noddy, I could change its habits from those of a "layer" to those of a "sitter." One can observe under such circumstances an almost immediate change in the general disposition of the birds. Before the egg is put down in the nest, the bird, which may be sitting on a nearby limb, will fly away at the slightest disturbance. When the egg is put into the nest, the bird on returning will alight near the nest and sit stolidly on a limb as before. Suddenly it is visually stimulated by the egg. It peers down at it, extending the head and withdrawing it, turning the head slightly to one side. It then alights on the nest. Contact with the egg seems immediately to change the disposition of the bird. The bird will now remain upon the nest, "rattling" in its gruff, hoarse way, and attempting to strike if one approaches too near. The reverse of the above behavior can be noticed if the egg is removed from the nest of some bird, even if it has been sitting on the egg for several days and consequently has had exercise in all the instinctive activities present during the brooding-season.

The sooty reacts quite differently to colored eggs. They were dyed with the same dyes as were the noddy eggs. These tests were made upon three separate parts of the island. The sooties on returning and finding the colored eggs exhibited signs of great uneasiness. They walked round and round them, poked them with their beaks, rolled them out of the nest and then rolled them back. In one set of tests the eggs colored with vermilion dye were absolutely rejected. In another set of tests, made with different birds, vermilion was accepted; green was not accepted in one case, but in two other tests it was accepted. The black egg was rejected in one case, but was accepted in two other cases. On the whole, each color and black was accepted, but in every set of tests at least one of the dyed eggs was rejected. In one case the bird whose nest contained the vermilion egg dug a new nest alongside of the old one and made nearly 100 trips between the old nest and the new. They, however, accepted each other's eggs and noddy eggs without question. One sooty sat down immediately upon its nest after a hen egg had been put there in place of its own. Several days later, on again examining this nest, I found that the hen egg had been pushed aside and a new sooty egg deposited.

From these experiments on the dyed eggs, it becomes apparent:

(1) Under the conditions of the above test the noddy is not at all affected by changing the hue, brightness, and markings of its egg.

(2) The sooty is affected by changing the visual appearance of its egg, but whether in the latter case the disturbance was due to the change in brightness or the change in hue or in marking, is not determined by the above experiments.

(3) Neither the noddy nor the sooty recognizes its own egg.

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TESTS WITH NODDIES ON RECOGNITION OF THE NEST AND NEST LOCALITY.

The nest of the noddy is not individually recognized. I found that I could exchange a large nest for a small one or *vice versa;* that I could tear out the old nest and construct a rough one of bay-cedar limbs, etc., without the noddy's reactions being in the least affected. I then made tests of the following kind upon the nest locality, one of which I shall cite in detail:

An isolated noddy nest, placed in the crotch of a limb near the stem of the bush, was moved 3 feet farther out on the limb, but was still left in plain sight. The noddy, on returning, flew to the old position of the nest. After some delay it alighted on the nest. It then flew back to the old position. It then flew to a limb a few inches above the old position of the nest and waited there for a time. It then made 9 trips between the old position of the nest and the new. After half an hour it settled down in the nest in the new position and remained quietly brooding the egg for a few minutes. It then became uneasy, got up, and made several more trips to the old position and back to the new. Finally it settled down upon the nest in the new position and made no further attempt to return to the old position of the nest. I next made it a nest out of bay-cedar limbs and put it in the old position, putting therein a sooty egg which I found at hand. On returning, the bird naturally had the choice of going to its old nest and its own egg in the new position, or going to a makeshift nest containing a sooty egg in the old position. It went immediately to the old position and settled down on the sooty egg with apparent satisfaction. These tests were repeated on other noddies with similar results.

I conclude from these possibly insufficient data that the nest locality exerts the stimulus for nest orientation and that the nest and egg as such are not important factors in this situation. Whether or not this return to the old position is accomplished in terms of visual data, my experiments do not show. Provided the one limb is left which supports the nest, the rest of the bush and the surrounding bushes may be cut away and the whole visual environment greatly altered without the birds' reactions being changed in the least.

TESTS WITH SOOTIES ON RECOGNITION OF THE NEST AND NEST LOCALITY.

The study of nest and nest locality recognition are the most interesting problems in the study of the life of the sooty. If one recalls the conditions under which they lay their eggs, namely, in open spaces and at distances apart sometimes not greater than 10 to 14 inches, one can not but admire the exactness and ease with which the sooty approaches its own nest. I have made numerous experiments upon the distance to which the sooty nest can be moved without disturbing the habitual adjustment of the birds to it. These tests, while not satisfactory as regards the determining of the sensory factors entering into this function, at least will serve to show the nicety with which the sooty makes its adjustments to the nest locality.

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Fig. 19. The strutting movements of the male Sooty.

Fig. 20. The two Sooties on the left of the cut are beginning to fight.

Fig. 21. Flashlight of Nesting Sooties To show possibility of studying behavior at night.

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EXPERIMENT I.

(*a*) An isolated nest under a bush was chosen for purposes of experimentation. Nest was left intact, but the egg was removed and placed in a new nest dug 18 cm. due north. Bird returned to the old nest and stood impassive. Attempted to settle down on the nest and to poke egg, then looked up and saw egg, crawled over to it and sat down upon it. Bird got up and adjusted the egg and nest elaborately. Time for adjustment to situation, 30 minutes.

(*b*) I then allowed the bird 30 minutes at the new nest. At the end of this time I scared it away and placed its egg back in the old position, putting another sooty egg in the nest I had made. Result: Bird went back to old nest and covered egg without so much as looking in the direction of the new nest.

(*c*) Experiment (*a*) was repeated with similar results.

(*d*) Twenty minutes allowed for repose after above experiment. New nest No. 2 was then made 18 cm. due west of new nest No. 1. Result: Bird went back to original nest, shaped the nest, and scratched around in it and then walked over to new nest No. 2 and sat down on egg after adjusting it.

(*e*) Twenty minutes again allowed bird in this position. I then frightened it away and noted the pathway of return. The bird walked by old nest, inclined toward it slightly, then walked on directly to the egg in new nest No. 2.

EXPERIMENT II.

A nest in the sand in an open space was chosen. A large tuft of grass was situated near. This made a very prominent visual characteristic. I pulled up the tuft of grass, obliterated the old nest (marking it with a pebble), making a new nest 88 cm. due north of the old, inserting the tuft of grass as nearly as I could in the same relations to the new nest as it stood to the old. Bird on returning *stood for 8 minutes at old nest, then put down beak and attempted to arrange the egg just as though it were present.* Later, bird walked over to the new nest, partially sat down, then got up and went back to the old nest, turned round and round in the exact position of the old nest, walked over to the new nest, arranged the egg, went back to the old nest, remained there at a loss for several minutes, turning head round and settling down with body exactly as though egg were present, then went over to the new nest and sat on the egg for a moment or two, then back again to the old nest. Finally adjusted the new nest elaborately and remained there in peace. I then frightened it away. On returning, it repeated the above reactions, but with fewer trial movements. A second time I scared it away; again it returned to old nest and tried to get contact with egg. This second time it stood at the old nest for a long time, fighting all the other birds away. Finally, at the end of 10 minutes again walked over to the new nest and sat down. I scared it away again after allowing it to sit on the new nest for 12 minutes. Bird gone for 30 seconds. On returning, alighted from the air exactly upon the center of the old nest and again tried to adjust to nest in the old way. At end of 1 minute and 35 seconds waddled over and sat down on egg in new position. Was driven away again after 10 minutes of repose. Again alighted upon old position. Repeated it again; again alighted on old nest, but this time left it for the new in 12 seconds. Again alighted near old nest, ran to it and stopped there for an instant, passing rapidly on to new nest. Again alighted on old nest, but

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found new in 10 seconds. This routine was repeated 16 times, practically an afternoon's work, without the bird adjusting itself perfectly at any time to the new situation.

I repeated the above tests on 3 other birds which were nesting out in the open spaces, with absolutely identical results. In other cases I found that the nests could not be moved in any lateral direction for more than a few centimeters without the birds being badly disturbed. As a control test to the above I obliterated several nests and then redug them in the old positions. In no case were the birds disturbed by this.

EXPERIMENT III.

A nest was chosen in an open space, but very close to some bushes. I obliterated the nest as the bird had constructed it, inserted a black pan, filled this with sand, and constructed a nest inside of it. This gave me an opportunity to move the nest *upward* as well as laterally. On returning the bird alighted on the nest without showing any signs of disturbance. An hour later I came back and pulled the pan out of the sand and put a few sticks under it. The bird returned, but was not disturbed by this slight change. I then drove in four stakes 10 cm. high and mounted the pan thereon. This served to raise the nest upward without disturbing the other relations of the nest. The bird on returning *alighted immediately on nest.* The other birds gathered around, craning their necks and peering upward. The bird then stood up and came to the edge of the pan and peered down. This seemed to disturb it and it flew to the ground, but hopped up again immediately, covered the egg and sat there in comfort the rest of the day. Raising the nest 10 cm. in the air requires almost no adjustment on the part of the bird. On account of a storm on the island, which lasted for 2 days, no further experiments were made at this time on this nest. I next raised this nest 100 cm.; *bird alighted immediately squarely on top of the nest;* did not make a false movement. On craning neck over the edge of the pan a little later, however, became disturbed and alighted on the ground, and remained there for 45 minutes without attempting again to get on nest. I forced bird to fly up. Again alighted on the nest and began to brood the egg in comfort. On my return several hours later it was still sitting quietly on nest.

On the second day after this (when this same bird was at the nest again) I lowered the nest back to 10 cm., its first vertical position. On returning the bird alighted squarely on the nest, making perfect adjustment. I scared the bird away. On its return the bird again adjusted accurately. I next moved the nest back to the height of 100 cm. Bird returned and alighted on egg and adjusted to it before I could get back to my position in the bushes. Adjustment in the vertical plane is made with exceeding rapidity and ease.

I then moved the nest 100 cm. to the east, leaving it 100 cm. above the ground. Behavior of bird very interesting. Would not alight on nest. Alighted at the former ground position. After a long time flew from the old position and up to new position of nest. Immediately hopped down and began a most peculiar performance. *Bird would hover in space, attempting to adjust to the nest in the air at its former position and height.* It would then fly away again and come back to the old position and try to alight in space. This was done 20 times. At the end of 20 minutes the bird

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alighted upon the pan in its new position and sat down on egg. I then scared the bird away, 5 successive times, to see if it would alight immediately upon the pan. Each time on returning the bird alighted at the old ground position and proceeded from this point to the new position of the nest.

I then put the pan back in its old position. Bird returned and alighted on pan immediately. In this position I then raised the pan to a height of 200 cm. This raised the nest well up above any of the surrounding bushes. This did not cause the bird the slightest disturbance. I forced it to make three or four adjustments to the nest in immediate succession. It made them all with equal precision.

I continued my experiments on this bird in a similar way for several days and by repeatedly moving the nest now to the east, now to the west, etc., I succeeded in getting the bird to the point where it would immediately adjust to the nest regardless of its position.[1]

As was the case with the noddy, I found that the nest environment could be markedly altered without the bird's being disturbed in the slightest so long as the position of the nest was not disturbed.

SUMMARY.

In the case of both the noddy and the sooty, the nest locality is the important factor, the nest itself being reacted to by virtue of its location within this locality. Since environment can be greatly changed without disturbing the bird's accurate adjustment to the nest, it is evident that if the adjustment is made in terms of visual data the visual environment which serves as the stimulus must be complex and have a wide extension. I am not prepared to admit from the above experiments that adjustment takes place in terms of vision alone.

SOME EXPERIMENTS ON DISTANT ORIENTATION.

In the present connection, I shall not take up in detail the various theories concerning the factors entering into distant orientation. Anyone familiar with the literature on the subject knows that the facts, as well as the theories, are in a chaotic state. I wish in the present instance to present a few facts bearing upon the subject. It is generally supposed that the homing pigeon possesses the function of orienting itself from a distance in a higher degree than any other animal. It is also supposed that even in the case of the pigeon training is necessary in order to get the bird to return to its home from a distance. The method[2] usually adopted is, first, to allow the bird to get thoroughly habituated to its cote; then at successive trials the bird is allowed to return to its nest from distances beginning at 0.125 mile, then

[1] These tests are all confined to a radius of some 4 to 5 meters. I had intended carrying the test further to see if I could force the establishment of so strong an association that I could move nest from one part of island to another, but a storm which continued for several days made it impossible to continue the work.

[2] Hodge: Method of Homing Pigeons; Popular Science Monthly, April, 1894, pp. 758–776.

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from 0.5 mile and so on. In a short time the bird, on account of the increasing distances to which it is carried, combined with its keenness of vision, establishes visual landmarks throughout an enormous territory. A well-trained carrier pigeon could thus hardly be taken into a neighborhood which would be entirely new to it. This presupposes on the part of the bird the ability to establish visual associations at an enormous rate. All the laboratory tests which animal psychologists have made upon pigeons so far seem to show that the pigeon has no extraordinary ability to establish such associations.[1]

It occurred to me that any migrating bird ought to possess the function of distant orientation. As a test I made the following experiments:

EXPERIMENT I.

Six noddies were captured one evening and marked characteristically and individually with oil paints. These birds were put on board the laboratory launch, which happened to be making a trip to Key West on the following morning. The nests of these birds were all close together and were tagged with a large card in order to facilitate observation. Two of the birds were released at Rebecca Shoal Light, 31.38 km. (19.5 statute miles) from Bird Key; two at Marquesas, 72.75 km. (44.75 statute miles); and two at Key West, 106.02 km. (65.8 statute miles).

I kept their nests under constant observation the whole day long. Naturally, since the birds had been without food for some time, and since I had no guarantee that they would immediately seek the nest after reaching the island, I expected the return to the nest to be irregular. The results were as follows:

The two Rebecca birds, released at 9^h 30^m a. m., returned about 12 m.

The two Marquesas birds, released at 2^h 15^m p. m., returned together at 4 p. m.

The two Key West birds were released at 6^h 30^m p. m. One returned at 7^h 30^m a. m. the next day, the other at 5^h 05^m p. m. These two birds, bearing out my statement that these terns do not fly at night, probably slept in the neighborhood of Key West and left early the next morning. A heavy gale and rainstorm set in very shortly after these birds were released and I doubted very seriously whether they would ever return. Apparently one of the birds was not affected by the storm, while the other was probably blown from its course.

The respective mates of these birds remained on the eggs the entire time, going neither for food nor water (?).

EXPERIMENT II.

Three noddies and two sooties (one of the sooties was known to be a male) were captured and marked as above. Their nests were likewise prominently marked. On the early morning of Thursday, June 13, these birds were put into a large insect cage and given in charge of Dr. H. E. Jordan, who was returning to New York. He carried these birds *via* the

[1] See Rouse: The Mental Life of the Domestic Pigeon, Harvard Psychological Studies, II, pp. 581–613, and Porter: Further Study of the English Sparrow and Other Birds, Amer. Jour. of Psy., vol. XVII, pp. 248–271.

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government tug to Key West. There food was purchased for them (minnows). At 3 a. m., Friday the 14th, Dr. Jordan boarded the Mallory boat *Denver,* which left at that time for New York. On board the boat the birds were both watered and fed. On Sunday, the 16th, at 9^h 20^m a. m., the birds were released at lat. 35° 8′, long. 75° 10′ (12 miles east of Cape Hatteras approximately). The wind was fair and fresh for several days after the birds were released. I kept their nests under constant observation, but had almost given up hope of their returning when, to my surprise, on June 21, at 8^h 30^m a. m., I found both marked sooties on their respective nests.

None of the marked noddies was ever found at its old nest, but several days after the sooties had been observed at their nests, by chance I observed one of my marked noddies attempting to alight on its nest. On account of the mate having formed new "affiliations" this was not permitted, and I immediately lost track of the bird.[1] I have little doubt that the other noddies also returned to the island, but likewise were not permitted to return to their nests.

The distance from Hatteras to Bird Key in a straight line is approximately 1367.9 km. (850 statute miles). The alongshore route, which is the one in all probability chosen by the birds on their return, since they were gone several *nights,* is approximately 1739.6 km. (1,081 statute miles).[2]

EXPERIMENT III.

On Monday, July 8, two noddies and two sooties were captured and marked and given into the charge of Dr. Hartmeyer, who was returning to Germany by way of Havana. The birds were in such poor condition, owing to the enormous strain of several days' feeding of their then quite large young, that we decided to release them at Havana instead of taking them farther out. On the 9th the birds were carried by Dr. Hartmeyer on board the Government tug and taken to Key West, where they spent the night and part of the following day, the 10th. They were carried in Dr. Hartmeyer's stateroom to Havana on the night of the 10th. Early in the morning of the 11th the birds were released in Havana Harbor. All returned to Bird Key on the 12th. Since they had had to spend three days without food or water, they were in poor physical condition. They probably spent one day and night around the shores of Cuba, leaving there early

[1] At one of the sooty nests the egg had hatched. The egg at the other nest had hatched before the bird was captured. Apparently the 2 sooties which were left at the nests cared for the young birds without aid from the outside, the young being simply left in the nest while the parent sought the food. The behavior of the noddies left at home presents an interesting contrast to the "faithfulness" of the sooties. After 3 days had passed, one of the noddies took a new mate. At the other 2 nests one of the most peculiar incidents of my stay was happening. These two nests were in the same bush, one about 6 inches above the other. Both the birds remained stolidly on their nests for 48 hours without going for food; they then began leaving the nest regularly for food and water, brooding the egg and feeding at intervals closely approximating the normal. Finally the bird in the upper nest began bringing food to the bird in the nest below. Each time on bringing the food, the bird from the upper nest would nod and bill and coo to the bird below—reactions wholly similar to those engaged in by newly mated pairs. The eggs in both nests were neglected, no effort being made to keep them constantly covered. Sometimes the bird from the upper nest would spend a half hour or more in the lower nest. Sometimes the bird in the lower nest would spend its time in the upper nest. Again at times both birds would be away from the nests simultaneously.

[2] It might be well to mention that the birds were transported in the hold of the *Denver.*

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in the morning of the following day. The noddies were observed on their nests at 7 a.m., while the sooties were noted for the first time at 6^h 30^m p. m., of the same day.

The distance in a straight line from Havana to Bird Key is approximately 173.8 km. (108 statute miles).

I think that these tests are significant. The return from Cape Hatteras is really startling. Cape Hatteras is hundreds of miles outside the range of distribution of the noddy and sooty terns. If my statement that the birds rarely leave the island for distances greater than 15 knots for purposes of feeding corresponds with the facts, it becomes extremely improbable that they could have formed visual associations throughout such a vast territory as that described in these experiments. While these experiments are not in any way crucial, the facts obtained from them are extremely difficult for current theories of distant orientation to explain.[1]

SOME PRELIMINARY EXPERIMENTS WITH SOOTIES UPON THE LEARNING OF PROBLEM BOXES.

In all the following experiments, small wire boxes were put down over the egg and the bird was forced to overcome certain difficulties before it could reach the egg. The experiments will show that this method could have been used with profit if time had permitted. On account of the difficulty of making suitable problem boxes, our experiments are of a very rough and ready kind.

Experiment I.

A simple labyrinth was placed over a sooty nest. This labyrinth offered only one blind alley, but the bird was forced to change its direction three times and traverse a distance of about 3 feet before it reached its egg.

The movements of the sooty when this situation confronts it are characteristic. It first takes up a position which offers the plainest view of the egg and then attempts to push its head straight through the meshes of the wire. Leaving this position, it walks around and around the labyrinth as a whole and makes no attempt to enter the open door, although the latter is made very prominent by virtue of its being marked with two large upright sticks. The first four or five trials consumed about an hour each, the birds working persistently most of the time. So little improvement was manifested and the test bade fair to consume so much time that I abandoned taking continuous notes upon it. I left the simple labyrinth in place, however. By the end of 3 days, both male and female had adjusted themselves perfectly to it and could go in and out with rapidity, but when

[1] When I left the island I carried a noddy to a distance of 40 miles in order to observe its behavior during the trip. The bird was turning in a circle, twisting, and poking at the mesh of the wire cage incessantly. The turns and movements of the vessel did not influence the movements of the bird in the least, so far as I could observe. When released the bird flew down near the surface of the water and started in the direction of home. Dr. Mayer informed me that this bird returned to its nest. Reynaud's law of "contre-pied" has in my opinion not the slightest basis in fact. In order to duplicate in reverse order on its return all the movements made on the outgoing trip the bird would have had to fly back, revolving mainly in a circle!

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I attempted to get accurate tests of their time the birds became excited and tried to go through the meshes as before.

EXPERIMENT II.

The following series of experiments was tried upon a marked male sooty. A cubical wire box, 35 by 30 by 25 cm., was inverted over the nest. A simple opening, 9 by 12 cm., gave access to the egg. This opening was placed due west.

The male on returning trotted round and round the box; found the door in 3 minutes; was uneasy; attempted to get out but could not find opening. Stuck his beak in and out between the meshes. Became excited and tore at the wire with beak for several minutes. A slight disturbance in the neighborhood at which the other birds flew up caused him to redouble his efforts to escape. Got out at the end of 14 minutes. Walked away for a foot or two, trotted in again immediately. Was uneasy and came out again, this time without useless movement. On trying to reenter a moment later, he missed the opening and went halfway round the box and returned before entering. Out again immediately. In returning again missed his way in and went three-fourths around the box, turned and entered. This time he turned the egg with his beak, but would not sit down upon it. Out again immediately. Entered after a few useless movements. Tried to come out again immediately, became confused and fought the wire. Stopped to adjust the egg, but again would not sit down. Came out again immediately, then entered and sat upon the egg, this time in apparent comfort. The box with its opening produced no further disturbance. Time for adjustment to new situation under above conditions, 30 minutes.

I left the box in position the rest of the day. On the following morning, since the marked bird was still on the nest, I carried this test further by piling up loose sand around the entrance. The bird on returning was not in the least frightened by the change. Went immediately to the door, but finding the sand, walked round and round the cage trying to force his way through the meshes of the wire. Tried to get into door again and again, but would not scratch at the sand. Divided his time pretty well between the east side of the box, where the egg could easily be seen, and the west side, where he had formerly gained admission. Bird was very persistent, but at times would walk away for a few feet and then run hastily back to the box and continue his useless movements. I then scraped away the sand so as to expose an inch of the opening. The bird alighted and passed by the door again and again. Apparently no perception of the situation as a whole. I then exposed two inches of the opening so that only two inches of sand remained in front of the opening. Under these circumstances, the bird mounted the sand pile again and again and attempted to peck his way through the meshes of the wire above the opening. Finally by accident he poked his head through the opening and squeezed through, making no effort to enlarge the opening. Time of whole experiment, 1 hour.

After 5 minutes I drove the bird away (lifted up the wire box and allowed him to fly) and piled the sand up to the height at which he had previously been successful. Time for adjustment: 1.16 minutes.

I next piled the sand up so as to completely cover the opening again. After 20 minutes of random movement and no success, I scraped away the sand so as to expose one inch of the opening. The bird came up and

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with great effort squeezed through the hole in 0.25 minute. I then removed all the sand and left the box in position as before. On the following day, since the unmarked bird (female) was on the nest, no further tests were made upon the male. On the second day from the above I continued my tests.

As in the last test, 2 days before, I first piled up the sand within an inch of the top of the opening. Time for entrance: 2 minutes.

I next piled up the sand so as to completely cover the opening. Finally, after 38 minutes of random movement, while attempting to poke his head through the wire mesh above the opening, he accidentally poked bill and head through the sand pile. Withdrew his head, walked round and round the cage as before, then came back to the hole and poked his head into it six or eight times. This was done apparently simply to get nearer the egg. Success at end of 40 minutes from the beginning of the test. He went to the nest and sat down. Apparently the nest did not suit him as regards depth, for he immediately began to hollow it out by scratching. Apparently the scratching impulse arises only when the bird is at the nest. I think it exceedingly curious that this reaction was not utilized in such situations as the above. No further tests were made on him that day.

Two days later I again took up work with him. I first tested him with the sand left one inch from the top of the opening. Time: 0.20 minute. I next covered entrance over completely. Result: Again many useless movements similar to the ones already described. Time: 7 minutes.

I repeated this. Almost no useless movements. Bird dived at once for the opening, made a small hole, pulled his head out, ran half way round the box and returning squeezed through the opening. Time: 0.66 minute.

Exactly the same procedure was followed with reference to the female with results identical, except that the female uniformly required more time to make the adjustments and was not so active and eager in her movements. From these experiments I concluded (1) that the egg and nest locality may be used in the place of food as a stimulus to the formation of new habits; (2) that the sooty tern can form associations by the trial and error method.

Experiment III.

After the above tests had been completed I tried the effect of placing the opening of the box in the other cardinal positions (no obstructions being placed to the opening). It must be remembered that all the adjustments of the bird had been made with the opening facing west. The opening was now turned due north.

Results: The bird (male) on returning went immediately to the west, stood for a second and then walked to the south; went back to west, then went to the east, then back again to the west, then went north. The moment he saw the opening he went into it and covered the egg. Time: 0.96 minute. Second trial: Alighted on west, but ran immediately to north. Time: 0.08 minute. Third trial: Bird alighted on south, swerved slightly toward the west, but ran immediately to the north and entered. Time: 0.10 minute.

The opening was then made to face east. Bird alighted at south, went to north by way of west, paused at north, then seeing door to the east dashed into it. Time, 0.10 minute. Second trial: Alighting south, ran to

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Fig. 22 The character and grouping of the Nests of the Noddies.

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west and fought the wire for 3 seconds, hesitated at the north, then dashed round to the east and into the opening. Time, 0.13 minute.

Opening was then turned south (the bird usually alights at the south). Result: First trial: Ran into opening before I could move away from the nest; not the slightest useless movement. Second trial: Ran into box before I could time him. I repeated the above tests on the female with similar results.

If the behavior of the birds under the conditions of the above test is contrasted with the behavior of the rat under conditions of a similar test, one is struck by the very great rapidity with which the birds make these adjustments. Turning the box as was done above and presenting it to the rat would have caused him the greatest difficulty. I conclude from this that the bird makes these adjustments largely on the basis of visual data, whereas in all probability the rat makes the same adjustment by means of kinæsthetic data.[1]

EXPERIMENT IV.

After these animals had been accustomed to having their nest covered with this box for some 2 or 3 weeks, it occurred to me that if the recognition of the nest is accomplished largely by means of visual data, they ought to react to the box, even though it were moved from place to place without being disturbed very markedly by the change so long as it was not carried outside of their range of vision from the point where they alight. The box was first moved 88 cm. due north (entrance west as usual), while the egg and nest were left in the old position.

Result: The bird (male) sat on the egg immediately without so much as looking at the box, which was in plain sight 88 cm. to the north. After sitting on the egg for a moment, the bird became uneasy, left the egg and went over to the box and entered it, and then returned to the egg. He repeated this procedure three or four times. On the last two trips, after entering the box and not finding the egg, went round and round the box. While he was doing this the female, which was standing on guard nearby (up to this time inactive, however,) rushed over to the egg and covered it. The male came back and drove her away and remained in comfort on the egg.

I then went to the box, scooped out a nest in the ground inclosed by it, and put in an egg from a nearby nest. Result: Returned and sat on his own egg, but craned his neck and peered at the box, showing evident signs of "interest" in the box.

I next removed his own nest, leaving the box as in the above test. Result: Bird ran first to box, then back to old position of nest. He turned round and round in this spot, attempting to find egg. He then dashed for the box, entered and sat on egg, but was not quite comfortable and kept peering out the door and into the corners of the box. He then got up, walked around the cage once or twice, came back to the egg and adjusted it, and sat down in apparent comfort. Time for this readjustment: 0.66 minute.

[1] Watson, John B. Kinæsthetic and Organic Sensations, etc. Monograph Suppl. Psy. Rev., No. 33, p. 85.

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If the behavior of this bird be contrasted with that of others whose nests had been disturbed (p. 225), it will be found that his readjustment to the nest in a new situation was very much more rapid than in the case of the former. Apparently, a partial but incomplete visual association had been established between the nest and the box. It is clear in this test that if recognition of the nest is not accomplished entirely by means of visual data, such data can nevertheless play the fundamental rôle under certain conditions.

EXPERIMENT V.

A heavy focusing cloth of rubber was placed over the box, leaving only the entrance, which was west, uncovered. The egg could be seen dimly, but the rest of the box was extremely dark. In order to see the egg the bird would now have to approach the nest and go very close to the door.

Result: Bird apparently frightened at the dark object as a whole. Hovered over the box, but would not alight. Finally alighted and went up to within one foot of the entrance and peered in. His reactions were very curious. Went over to east corner of cage, peered at the covering, then backed off. Approached the entrance and peered in. Started in, but his courage deserted him. He did not go round and round as formerly. This probably was because the visual stimulus of the egg was cut off. He finally poked his bill into the door, pulled his head back, then began a curious procedure of flying 10 feet away and flying back to the nest, repeating this in rapid succession. In conscious terms, this behavior suggested that the original orientation was in some way recognized by the bird as being wrong, and that by leaving and again approaching the bird sought to secure better orientation. This lends support to my statements above that if the stimulus to the nest depends upon visual factors the latter must be complex. The bird then came to the door, stood near it, poked head in and withdrew it, repeating this 15 times without moving from his position. At the end of half an hour he entered and stayed for a moment, but rushed out again. Entered two or three times again, but would not remain. At the end of 45 minutes, after many such timid entrances, the bird walked in and sat down in comfort. I scared him away. He returned immediately and brooded the egg. He had become entirely adapted to the changed conditions.

These experiments, inconclusive and unsatisfactory as they are, nevertheless show that a definite question has been raised concerning the *modus operandi* of nest recognition and nest orientation, which is entirely open to experimental treatment. They likewise show that the nest locality, whatever may be the stimulating factors present, may be used at will as a stimulus in controlling the reactions of the birds.

SOME PRELIMINARY EXPERIMENTS WITH NODDIES UPON THE LEARNING OF PROBLEM BOXES.

A few experiments similar to the above were tried on the noddies. A cubical box, 45 cm. to the side, made of wire mesh (12 mm.), was inverted over the nests of noddies built near the ground. A 9 by 12 cm. opening was inserted in one side of the box on a level with the top of the nest. The

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noddies were allowed to accustom themselves to entering and leaving the nest by way of the opening. When they had become thoroughly accustomed to the box it was possible to interpose obstacles in the way of their adjustments to the nest, by putting certain simple obstructions at the opening. Only enough tests were made to prove the applicability of this method for controlling the reactions of the noddies. The following extracts from my notes show the behavior of the birds in adjusting to the box when no obstructions were interposed at the door:

Both birds present (one marked). They alighted on top of the box and attempted to poke heads through the meshes of the wire. After 15 minutes of random effort, the marked bird found the entrance and immediately covered the egg. I scared this bird out and before it returned the unmarked bird found the entrance and covered the egg. Both birds adapted themselves to the situation very quickly.

After allowing the birds several days in which to get entirely accustomed to the box, a white bristol board sector was inclined at an angle to the cage entirely covering the entrance when approached from the front. The end of the cardboard, which rested on the ground, was pointed so that when the cardboard was struck or pushed it would fall over, thus exposing the entrance.

First trial: Bird alighted on a limb very near to the entrance and stood for a moment, then flew away. Returned and alighted as before, opened its mouth and gazed at the egg in a stupid, inert way. After standing for some time the bird again flew away and again returned. This was repeated four times. It then began flying away and returning to the top of the cage. This behavior of flying out over the water and returning to some new position on the cage was repeated many, many times. At last it alighted on the perch and stuck its beak in at the crack made by the cardboard's being inclined at an angle to the opening. By degrees the cardboard was pushed aside and the bird entered. Time: 41 minutes.

Second trial: (10 minutes later). Flew against the cardboard, attempting to insert beak at the same time. Repeated several times. This was a clumsy but ingenious method. Time: 15 minutes.

Third trial: (One day later). Alighted on top of the box, flew away, returned, then flew at the door as in the last test, pecked in a slow and foolish fashion, finally pecked it open. Time: 1 hour.

Fourth trial: (10 minutes later). Many trial movements as in the above case. Time: 1 hour and 15 minutes.

Fifth trial: (One day later). (Egg had hatched during night.) Bird flew at door, mate sat stupidly on top of box. Flew against the door again, finally opened it by this means. Time: 13 minutes.

Sixth trial: (10 minutes later). Many useless movements as before. The bird still attempted to remove the obstruction by flying against it. If this failed it fought at the wires on top of the cage. Mate stood stupidly on top of the box the whole time, but made no effort to imitate, follow or assist the marked bird. The cardboard was finally knocked down with the wings. Time: 16 minutes.

Seventh trial: (One day later). After flying against it several times the cardboard fell. Time: 6 minutes.

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Eighth trial: (Immediately afterwards). Very definitely done. Time: 3 minutes.

Ninth trial: (Immediately afterwards). Shoved cardboard aside with beak. Time: 0.16 minute.

Tenth trial: (Immediately afterwards). Opened with beak. Time: 0.16 minute.

The above experiment was repeated on the mate (unmarked) of this bird. Its time was very much better than that of the marked bird.

First trial: Flew against the cardboard and knocked it over immediately. Time: 5 minutes.

Second trial: Flew against it vigorously. The wind assisted it. Time: 7 minutes.

Third trial: This bird worked ten times harder than mate. Flew against the cardboard very definitely. Time: 3 minutes.

Fourth trial: Not a useless movement. Time: 0.10 minute.

Fifth trial: Interrupted work twice to drink. Time: 3.50 minutes.

The above trials were all given on the first day and in immediate succession. This change in method was necessitated by the increasing shortness of my stay.

Sixth trial: (One day later). Flew against cardboard, the wind aiding it. Time: 1.50 minutes. On account of the wind, no further tests were made that day. The heavy winds continued for six days and the experiments had to be discontinued.

Seventh trial: (Six days later). Opened by flying against it. Time: 6.50 minutes.

Eighth trial: Opened by flying against it. Time: 9.68 minutes.

Ninth trial: (One day later). Time: 7 minutes.

Tenth trial: Time: 1 minute.

Eleventh trial: Time: 0.75 minute.

No further tests were made on this bird. Useless movements were rapidly eliminated during the first five trials given on the first day. Apparently these five tests and the one given on the following day were not sufficient to fix the association definitely enough for it to be carried over the six days in which no trials were given. The test is suggestive of a very low order of retentiveness.

Other problems were submitted to the noddies in a similar way, but the results were not sufficiently definite to report. In conclusion, however, we may say that the above method ought to be one of great importance in observing the reactions of the noddies under conditions of control. By it I am sure that in the end we may gain a knowledge of the variety and the complexity of the problems which the noddy can learn. The method would work equally well with respect to the length of time which such associations can be retained.

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THE DEVELOPMENT OF THE YOUNG NODDY IN CAPTIVITY.

The following study of the development of the young terns in captivity is based both upon field observations and upon the observation of young birds reared in captivity. I was enabled to rear 3 young noddies and 8 young sooties from birth to 30 days of age.[1] At the end of 30 days they were still in good health, but I was forced to leave the island on the 18th of July, consequently my observations are concerned only with these first 30 days of the life of the young terns.[2]

On account of the great difficulty of securing suitable food, the rearing of the young terns entailed enormous labor both on my own part and on that of my servant. Each morning it was necessary to take a seine and a power-boat in order to catch a supply of minnows for the day. During the first few days of their lives, the young terns can swallow only very small, perfectly smooth fish. In order to keep the fish in good condition it was necessary to tow a live-fish car with us, into which the minnows could be emptied as soon as caught. During the first week, the young birds were fed about five times a day. This consumed an enormous amount of time. Each bird had to be fed individually and only one fish at a time could be given. When one considers that a young, live, healthy tern can eat from 12 to 40 minnows a day, depending upon the age of the bird and the size of the minnows, one can form some notion of the labor entailed in rearing the birds. The main difficulty we experienced was in catching the fish. On stormy days it was almost impossible to seine successfully, and even on some fair days, for some inexplicable reason, the fish were not to be found near the shore on any of the islands. As the season advanced, the minnows became scarcer and scarcer. The fact of the increasing scarcity of fish during July and August will be a serious handicap in the future for anyone who may desire to rear these birds and observe their growth for a longer period of time than the above.

First day:

The young noddies began to appear on the island about June 9 (1907).[3] The first few hours after birth they are extremely helpless. During the first day of their life they exhibit few signs of fear, making little effort to shrink away from the hand. However, their eyes are very mobile. The 8 young birds which I observed on the first day were able at 5 hours of age to maintain the head and body fairly well in a standing position. At the

[1] I began with 8 noddies and 12 sooties, but owing to my attempting to feed them upon "salted fish" during a scarcity of live fish, 5 noddies and 4 sooties died.

[2] The photographs of the young terns serve roughly to show some of the stages in their development during the period in which they were under observation. Sooties 1 day, 3 days, 8 days, and 30 days of age are shown on plate 3. Noddies 1, 3, 18, and 30 days of age are shown on plates 4 and 5.

[3] About 65 per cent of the young are born with black plumage, the other 35 per cent are born almost pure white. Thinking this might mean a sexual difference, I asked Dr. Charles R. Stockard to make an anatomical investigation. It appeared that the color at birth is not correlated with sex.

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end of the first day the birds were able to stand fairly erect and to move their heads with some freedom, following my pen-point with both head and eyes when it was moved in front of their heads. When taken from the nest and put upon the floor, the birds showed a marked tendency to shrink when the shadow of the hand was thrown across the head. As I write with one upon the table before me, it is pecking vigorously at my fingers. Pecked once at a large spot on the table, then at its toe. They show no fear at being handled. They can not swim at the end of the first day. They were tried first in fresh water. No coördination of limbs was present. Head could not be held up and birds began to sink rapidly. Water caused defecation in one case and disgorgement in another (they had been left with the parent for 5 hours). The movements used in disgorgement were as rhythmical and perfect almost as is the case with the adult. The birds yawned a great deal (the same is true of adult noddies and sooties). This reaction is quite different from that used in opening the beak for food. While yawning they will not accept food. The note of the young noddy is very different from the hoarse, rattling sound of the adult. It is a soft, liquid, slow, plaintive "querk-querk-querk."

The huddling reaction[1] is present the first day. The birds all huddle together after being separated. They lower their heads and attempt to nestle under the bodies of their companions. At the end of the first twelve hours these birds are the superiors in the point of development of the sooties, but the sooties very rapidly outstrip the noddies.

All of these reactions which are present in the young bird on the first day are of vital importance to them, with the possible exception of yawning (even this reaction, apart from its possible value in respiration, may be of value in strengthening the musculature of the jaws, etc.). It is absolutely imperative for them to have the free use of the head and eyes and to be able to stand erect and to peck during the first day. The feeding parent on returning alights near the young bird, puts down its beak, and successively touches and taps the beak of the young bird, then its part of the reaction is at an end, provided by successive disgorgements it keeps its beak and throat filled with small minnows. The young bird must stand up and strike the beak of the parent until the parent opens its beak sufficiently wide to admit the beak of the young bird. When the fish in the mouth of the parent come into contact with the buccal cavity of the young, the swallowing reflex follows perfectly. The pecking of the young birds at the objects in their surroundings is not at first a pecking in the sense that the little chick pecks. It is rather a striking reflex. By means of it the young bird gains access to the mouth and throat of the parent.

The huddling reaction mentioned aboye is of value by reason of the fact that it gains for the young bird the protection of the parents' body from the cold of the northeast trade winds which set in at night. It is not a protective reaction in the sense of hiding from an enemy.

Second day:

The young noddies were kept day and night in a box which was covered by a cloth. They are extremely quiet all the time. At first they are small eaters, consuming rarely more than three minnows of small size at a feed-

[1] Not the true gregarious reaction in all probability. It was the normal mode of reaction to the parent.

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ing. With birds in captivity the visual stimulus alone is not sufficient to produce all the movements necessary to feeding. They do not raise their heads and open their beaks wide as do the young sooties. The food has to be placed on a level with the head, then at gentle tapping, the beak begins to open. There grows up a very rapid tendency on the part of the bird to work a fish into such a position that it can be swallowed head first. I found that their aim in pecking was not very accurate. Even after they are stimulated to begin striking at the fish with open beak they will strike above or below it, nor do they open the beak commensurately with the size of the fish. Apparently both sensory and motor sides of this visual-motor reaction need strengthening. Whenever the bird is disturbed, or when it is being fed, it continually emits the above plaintive little note. It is instantly hushed if the hand is placed over it. It huddles under the hand, turning, however, so as to keep the head and beak out (a characteristic reaction when under the breast of the parent). Coördination in walking is apparently little further advanced.

Third day:

The birds eat more freely, but their appetites are in marked contrast to the sooties of the same age. The movements of the noddies in taking food from me are still not perfectly coördinated. They are better able, however, than a sooty correspondingly young to swallow a minnow taken crosswise into the mouth. The birds are still very quiet. In the early morning, while the young sooties kept in captivity are raising a noisy chorus, not a sound comes from the noddies.

The birds were tried again in the water. This time the leg movements were fairly perfect. The head and neck were kept well above water and they managed to swim until the down became soaked. When the bird began to sink and water was taken into the mouth, disgorgement took place. A good deal of increase in strength was noticed in the movements of the wings, neck, and legs. Birds were observed pecking both at the ground and at one another, but as yet no fighting was noticed.

Fourth day:

The birds are eager for their food. Feeding from me, however, is still not perfectly done. My finger is often pecked at in place of the fish. They peck more frequently at one another, and I noticed for the first time one pecking at the fish another was trying to swallow. When one bird is fed at the edge of the box, the others immediately begin to crowd up near my hand. Either there is a following instinct being exhibited here, or else an association has been formed.

The birds were taken to the sand and put down. They moved about very slowly. I separated them about 15 inches. In 10 minutes all had collected into one group and stood huddled together. Up to the present time there is no association established between a call on my part and a hastening toward me or an answering call on theirs. The sooties very soon learned to answer my call by running toward me and giving vent to a lusty "peep."

Their sleeping attitudes were observed for the first time. They lie with the ventral surface of the breast down; head stretched out and turned to one side, sometimes both legs stretched out, sometimes only one. They were noticed to-day preening their feathers by movements characteristic of the adult. This was a very complete act.

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Eighth day:

The 5th, 6th, and 7th days are characterized by the appearance of the fighting reaction. This is full-fledged and well coördinated. From this time on I had to exert great care in keeping the young birds from injuring one another. Fighting is indulged in at any and all times unless the birds are covered. Apparently there is never any cause to evoke this reaction other than the mere visual stimulus of a bird nearby. On the 8th day the birds began to hop down from the box (a height of 3 inches) and to run to meet me.

Ninth day:

The birds have formed a great attachment for me. They will follow me all around the room. It is becoming more and more difficult to keep them in any box. They will clamber up to the top of the box if any means are at hand and will jump down from a height of 8 to 10 inches.

Eleventh day:

Birds are now forced to eat without any assistance from me. They learn this more rapidly than do the sooties, for the reason that the adult noddy in feeding its young sometimes disgorges the food upon the rim of the nest. The birds soon learn to pick up the fish from the floor, regardless of whether the fish are squirming or still.

Twelfth and thirteenth days:

These days show a notable strengthening in all of their instinctive responses. They peck frequently at small objects and have much more accurate aim. They rarely take the object into the mouth. The fights are now prolonged and furious. From further observation of the birds in the field I find that the pecking reaction is utilized by the young birds in *controlling* the movements of the parents. By means of it the young birds force the parents to cover them. When I cover the young birds with the hand they stop pecking. If I so arrange my fingers that they can not huddle underneath my hand, they continue striking it until the proper movement on my part is made to admit the bird under the cover of the hand. Once it receives the extended contact of the hand it gives a contented little "querk," which causes the others to hasten up and to huddle underneath the hand.

The nest habits of the birds of this age and older were noticed to-day for the first time. The nest is kept clean by means of their peculiar habits of defecation. The bird usually remains in the center of the nest. When defecation becomes necessary the bird backs quickly to the rim of the nest, stops suddenly, and forces the fecal matter far out over the rim (sometimes 8 to 10 inches). The interior of the nest is never soiled.[1]

The birds in captivity, even when on a perfectly smooth floor, held to the same habits of defecation. The birds were turned loose on the floor at this age. They began pecking very definitely at all small objects in sight, for example, my tan shoe-lace, a spot on the toe of my shoe, grains of coral sand, bits of feathers, strings, small sticks, and matches. No attempt was made to swallow the small articles except in the case of the match. Three birds did attempt, however, to swallow this.

[1] I have seen an adult noddy when defecated upon by another bird fly immediately to the water and begin bathing.

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Fig. 23.

Fig. 24.

Group activity of Sooties. Favorite sunning-place.

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One interesting fact, which bears out the contention of Lloyd Morgan, became increasingly apparent. The birds at first show no discrimination with reference to the objects at which they peck. I cite one instance in detail: One bird defecated upon a white surface. A second bird ran up, struck at the fecal matter, and got a quantity of it in its mouth. Movements characteristic of "disgust" took place. The bird finally shook the material out. A little later the same bird came up to the fecal matter again, struck it this time lightly, and again shook its head and wiped its beak. About 30 minutes later this bird approached it a third time. Bird shook its beak violently before it came within half an inch of the object and turned away without further noticing the fecal matter. Two days later, in a similar situation, bird again was stimulated by fecal matter, but turned away before striking it. Many others of the birds were stimulated by this material, but while they were often at the point of striking at it, they always inhibited the movement so that the fecal matter was never taken into the mouth. They had in all probability already made the discrimination.

On the thirteenth day a rather interesting association was set up by one of my birds. In the bottom of the box (14 inches in height) in which I was now keeping the birds, an old pair of trousers had been thrown with one leg extending over the edge of the box. One bird climbed up the trouser-leg and jumped down to freedom. This bird began scrambling out of the box as fast as I could replace it. None of the other birds imitated this one or ever escaped from the box by this method.

Sixteenth day:

A rather interesting development of the pecking reaction was noticed to-day. Small twigs of cedar, matches, etc., were pecked at by the birds and retained in their beaks. They made no efforts to swallow the sticks, but would walk around the room with them with head extended, a complete replica of the adult noddy throughout its nesting season (see p. 200). The birds were tested on cooked "Cream of Wheat." They struck at it eagerly at first, but soon learned to reject it in a manner quite comparable to the learning of the rejection of fecal matter.

Nineteenth day:

There is a very noticeable increase in the ability to use their wings. They are beginning to flop the wings and to use them in obtaining equilibrium. They use them quite noticeably now when jumping down from a height. The characteristic movements of wing and leg of the adult when dozing on a limb in the sun were noticed for the first time. The wing turned to the sun is drooped so as to shield the body, while the opposite leg is stretched out, the body being supported by one leg.

Beginning on the 16th day[1] and during the rest of my stay on the island the birds were fed only in the maze. At this age it becomes possible to use food as a stimulus in controlling their reactions. The statement of the behavior of these birds in learning the maze will be given later on.

The young birds in the field are slightly more developed at 19 days of age than the birds held in captivity. I captured 3 of these birds at about this age,

[1] The nodding reaction (p. 196) was noticed first in a perfect form on the 27th day. Two birds were fighting; after a vicious thrust No. 1 backed away from No. 2 and nodded vigorously. Fighting adults often do the same.

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but found them quite intractable. They were thrown into a state of absolute terror every time I approached them. I kept them in captivity for 72 hours, but they would neither eat nor drink. They fought me with all the vigor of an adult. Fearing their death from starvation, I returned them to their respective nests. The instinct of fear develops very early in these young birds in the field. Even at 3 days, if one approaches a nest containing a young noddy and attempts to pick it up, it will first disgorge and then strike vigorously with its beak. It is almost impossible to tame either the young noddy or the young sooty unless it is reared by hand from the first day. Lloyd Morgan, Spaulding, and others are unquestionably right when they affirm that young birds if taken early enough and reared by hand exhibit little signs of fear.

THE DEVELOPMENT OF THE YOUNG SOOTY IN CAPTIVITY.

The young sooty is born in a very helpless state.[1] On the 7th of June I took 8 young sooties, all born on that day. They differed slightly as regards their development. This is due to the fact that the birds dwell for varying lengths of time in the shell after it has become pipped. I have been passing through the bushes when the eggs were beginning to hatch and have heard quite lusty "peeping" and on looking about to discover the young bird have found that the noise came from birds still in the shell. Whether they are fed at this age or not I do not know. Sometimes they live as long as 2 days in the shell with only the beak protruding. At this stage in their development they make no response to the warning cry of the adults as they do later on. They go on "peeping" lustily after the adults have flown. The peculiar protective attitude of the young birds has been mentioned already; that is, the ability to lie outstretched and perfectly motionless. If left for a time in this attitude, they begin to "peep" as soon as the sun's rays become oppressive. This means of protection persists until locomotion makes possible a more effective method. When the protective attitude disappears and locomotion becomes possible, the bird runs to cover when disturbed. Hiding is never in any sense complete. Indeed, the reaction seems to be almost thygmotactic. The moment the young bird can put its head in the crotch of a limb or get its body in contact with some solid object, locomotion ceases.

First day:

The young birds which I captured showed apparent signs of fear. Moving the hand rapidly near them, as in offering a piece of fish, caused them to dodge quite noticeably. The instinctive cry is a lusty "peep-peep." They are well developed, but clumsy. The wings droop and the birds have difficulty in standing; coördinated sitting positions likewise are almost impossible. The birds are somewhat hard to feed during the first day, but

[1] For supplementary description of field behavior of young and parent see p. 215.

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after this age this process is easier with them than is the case with the noddies of a corresponding age. In the case of the sooties, as was not the case with the noddies, the mere sight of the food will cause the bird to open its beak. Light contact will likewise cause beak to open. Once the food gets into the mouth the rhythmical movements of swallowing follow perfectly.

Some locomotion is possible. They take a few wobbly steps with wings down and legs wide apart. Fairly well coördinated swimming movements are present, but the heavy down with which their bodies are covered soon causes the birds to become water-logged and they consequently sink. As the salt water begins to enter the mouth the bird raises its beak higher and higher and shakes out the water vigorously, crying lustily the while.

One of these young birds had not emerged from its shell; only its beak and the base of the beak protruded (eyes being covered by a membrane). Almost any call from me would cause this bird to "peep." Small minnows were offered and swallowed. The contact of the minnows caused the beak to open. I removed the shell; the bird made adaptive movements as if completing the process itself. After removal the bird was very insecure in its movements.

Second day:

The difference in growth is remarkable. Locomotion must have improved 100 per cent in the 12 hours. Birds can waddle around rapidly and maintain upright position fairly well. They follow moving objects with the head and eyes quite easily. Will dodge very quickly if hand is suddenly extended toward them: Some tendency present to nestle under one another, under my hands, and under the folds of the cloth. Birds are beginning to peck at one another, the raw wings being the spot usually attacked.

Feeding is quite easy. Moving the finger, fish, or bits of straw rapidly across the beak will cause the beak to open wide. Whole minnows are swallowed with ease. The birds sleep a great deal of the time. The adult birds flying over the experimental cage and calling are invariably answered by a "peep" from the young birds. Even on the second day feeding is an active process with them. A fish dangled in front of them will cause them to strike at it. If the beak fastens upon the fish in the center of the body the young bird by a peculiar shake and twist of the head will suddenly right the fish and swallow it head first. It is safe to say that at the end of the second day the young sooty is sufficiently developed to take any fish from the beak of the parent which is likely to be found there.

Even at this early age the birds are found pecking at one another's mouths or at a piece of food which another is swallowing. Pecking at one another in a way forceful enough to suggest the beginning of the enormously important fighting instinct was, however, not noticed up to this time. Any signs of fear which might have been present the first day have entirely disappeared by the end of the second.

Third day:

The birds have begun to run toward me when I approach them and call. They will lustily answer my "peep" at any hour of the day or night.

The fighting instinct appeared to-day in almost completed form. Two of my young birds faced each other and began striking simultaneously. A hold is taken on the body and maintained with grim determination, the

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victor all the time shaking his opponent as does the adult. Not the slightest sign of play has yet manifested itself. The birds as yet show no discrimination as regards what objects they peck at. They are as likely to attempt to swallow my finger as the fish. Very minute objects, however, such as specks and hairs (as is the case with chicks, according to Lloyd Morgan) are not noticed by them.

Fourth day:

I was awakened at dawn by the lusty "peeps" of the birds (I slept in a hammock about 10 feet away from them). When I "peeped" back the birds answered in a persistent chorus. Other sounds, which I made to test whether the above note was a discriminated auditory stimulus, were not answered when I made them higher or lower, or if they differed widely in clang quality. The birds, however, would answer the "peep" of other men if it were given at the usual pitch.

The birds are healthy and larger than those in the field. Three birds, 3 and 4 days of age, were taken from the field to compare with the birds reared in captivity. These birds were exceedingly wild, and although I kept them in captivity for 2 or 3 weeks, while they showed improvement in this respect, they never wholly lost their fear of me.

Their sleeping and lounging attitudes are very striking. In most cases, after a full meal is taken, the birds go to sleep. When lying down one leg (at times both legs) is stuck out so as to give the ventral surface of the body contact with the ground. Head is completely outstretched and laid on one side; eyes are closed. At other times the bird rests its rump on the ground, using legs as a prop, and dozes in this attitude. As it dozes its head falls to the right or to the left or vertically downward between the legs. When the beak strikes the ground the eyes are partially opened, the head is raised again and the process is repeated.

Fifth day:

I began training the birds to-day, to get them to form the habit of coming to a certain place for food and eating without assistance from me. The test was very simple. A dry-goods box 8 inches in height had an inclined plane, 2 feet in length, leading from the top to the floor. The birds were to be fed on top of the box.

I first put a bird upon the inclined plane and dangled fish in front of it, attempting to toll it upward. At first the bird would stand in its tracks, extending neck and head to strike at the fish. After trying this upon all of the birds I would pick them up, place them on top of the box, and there feed them. At the end of the third feeding the birds had begun to clamber up the plane. Walking upwards at this angle gave them some difficulty. They looked intently always at the fish and paid little attention to their own movements; occasionally mishaps such as falling from the plane occurred. At the end of the third feeding it was still necessary to start each bird by placing it on the inclined plane. No attempt was made by the other birds to follow the bird which was being tolled to the top of the box. The birds still show no discrimination as regards their food. They will swallow almost anything. I tested them with several different kinds of fish, small crabs, strings, and sticks—whatever was presented was swallowed unless care was taken to prevent it.

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Sixth day:

There is slight improvement in getting to the top of the box. The birds are still very clumsy, but are becoming more and more eager.

Seventh day:

Birds eager for breakfast. Two walked up the platform before the fish were shown. Two others came up as the first two were being fed. Live fish were given them to-day. The birds' movements are wonderfully fast. The extremely rapid movements of the fish are not faster than the action of their beaks.[1] There is little improvement in discrimination to be noticed. To-day, while I was feeding some of the birds, I felt a tug from behind, and on turning around, I found that one of them had swallowed about 3 inches of my handkerchief and was straining every muscle to force the rest of it down!

At the second feeding on this day one bird ran immediately up the plane and three others followed. When fish were presented these four birds began fighting vigorously. By the time they were fed, all of the other birds had clambered to the top.

The young birds were offered lemon peel to-day. It was snapped up by all the young birds eagerly. They continued to snap and swallow the lemon rind for three to four trials, and refused thereafter to open the beak for it.

Fighting is furious and prolonged. The young birds are exact replicas of the old in this respect. All that is necessary to start a fight is for one bird to come within striking distance of another.

Eighth day:

The association of walking up the plane to feed was perfect in all of the birds by the end of the last feeding on this day. They, however, had not yet learned sufficiently well to feed without assistance from me.

The young birds began to-day to dig holes in the sand, using exactly the same movements which are employed by the adults in digging the nest, except that the young birds do not shape the hole with the breast as the adults do the nest. By digging such a hole, the bird secures a surface which is damp and cool. The holes are usually dug near some solid object, whether because of greater coolness there, or through some thygmotactic tendency, I am not able to state.

A new instinctive reaction was observed to-day which is continued from this time on. A bird standing still will suddenly hop an inch or two in the air and come down in the same spot. As it descends it flaps its wings. The value of this reaction in strengthening the wing muscles is apparent.

[1] An old sooty with a broken wing, which had learned to come to the experimental cage when the young birds were being fed, was carefully watched to-day. Live fish were put down before it in a shallow dish. The bird would catch the fish near the middle of the body and by a quick flirt would bring the fish around head end first before swallowing it. This bird's movements were extremely quick. If I offered it a fish after it had been sufficiently fed, it would strike at the fish, take it in the beak, and then let it fall. Young birds were seen to do this early. The old bird would eat any variety of small fish but rejected sticks, grass, etc., after taking them into the beak. Lemon rind was offered. The bird took it into the beak but quickly rejected it. Would not take it a second time.

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Ninth day:

I began feeding the birds in Porter's[1] simple maze. The description of their behavior in learning this maze will be given further on in the paper.

Detailed records of the development of these birds were kept until they were 30 days of age, but on account of the great similarity of these later records to the above, I shall not cite them in detail. Experiments on learning to discriminate were made from day to day, but all such tests gave results very similar to those which have already been described. After the birds had learned to pick up the fish from a dish, it was possible to put seaweed, grass, bits of coral, etc., in with the fish. At first these were taken eagerly, but after a few trials the birds would learn to take the fish and leave the débris. Discrimination, however, never became very accurate. When very hungry, the bird would attack objects other than the fish. I think this is but natural, since the young bird feeds entirely from the beak of its parent until it is able to fly and fish for itself. They certainly get nothing there which would tend to develop discrimination.

It may be of interest in this connection to say a few words about the way the young birds in the field and those in captivity spend the greater part of their time. I have already remarked upon the fact that there are no signs of play. This was as nearly true of the birds in the field as of those observed in captivity. The only reaction which it is at all possible to consider a playful one is the one already mentioned, namely, the frequent hopping up and flapping of the wings. There is a question in my mind here as to whether after all Gross's theory of play fits the facts in any other genus of animals so well as in the case of mammals. Certainly the facts which I could gather with reference to both the noddy and the sooty terns do not lend support to his theory. These birds certainly lead an instinctively complex life. Surely the picking up of a live fish darting over the surface of the water is as complex an act as the catching of a mouse.

The greater part of the time is spent in doing *absolutely nothing*. The birds will lie outstretched in their sand-holes, getting up at times to stand stockstill for an hour or more, or to doze with head bent down. At intervals they peck at their feet and occasionally preen their feathers. In the field the routine is broken by the call from the parents which have returned to feed the young. At other times the young bird gets hungry; at such times it begins to cry lustily and to go up to the parent (which is likewise standing or fighting in the neighborhood) and begs for food by "peeping" and by striking at the parent's beak. Getting nothing, the bird will wander off for 10 to 15 feet into the shade and lie down again. Frequently it engages in fights with other young birds. Occasionally it will attack an adult noddy which has dropped down to gather sticks. The young sooty never attacks an adult sooty.

[1] Op. cit., p. 253.

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As the birds get older they begin to fly short distances. At the end of 35 days[1] they can cover 30 to 40 feet very rapidly by a series of flying hops.

THE BEHAVIOR OF YOUNG BIRDS IN CONTROLLED SITUATIONS.

After the young noddies and sooties had learned to eat without assistance from me they were allowed to learn Porter's simple maze. A cut of this maze is appended.

In place of admitting the birds to the maze at the entrance *O*, as Porter did, they were put down at *H*, and allowed to come out at *O* and walk up,

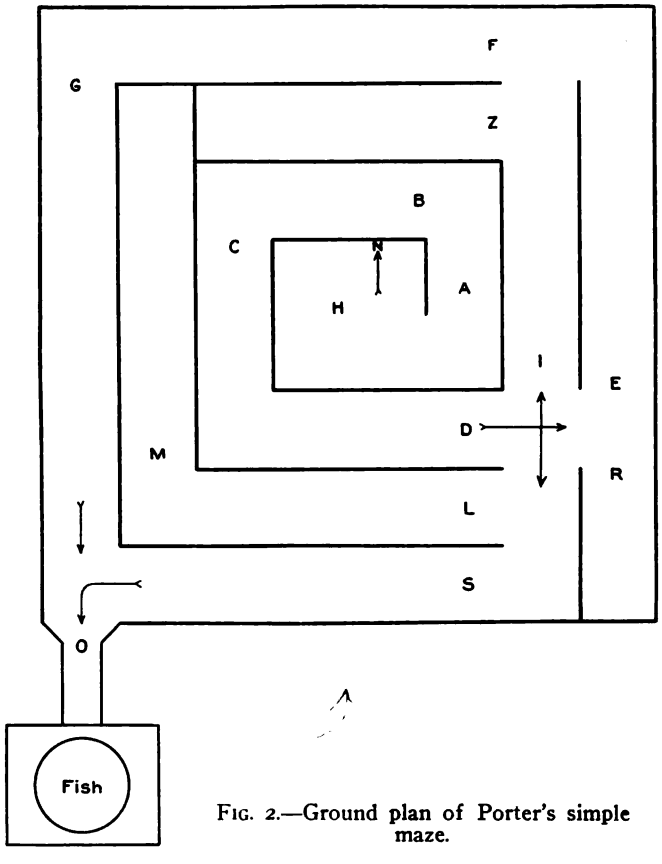

FIG. 2.—Ground plan of Porter's simple maze.

by means of an inclined plane, to the top of the box from which they had previously been taught to feed.

The dimensions of the maze were the same as those used by Porter. The

[1] This was the most mature young bird on the island. I had taken the precaution to mark the time of the appearance of the egg in several nests early in the season, in order to have the reactions of the birds in the field to compare with those obtained from birds in captivity.

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maze as a whole was 4 feet square; the alleys were constructed of white bristol board and were made 5 inches high and 5 inches wide. The top was covered with 0.375-inch wire mesh. The bottom of the maze was of wood. In order to determine more accurately the number of useless movements, fine white coral sand was sifted over the bottom of the maze to a depth of 0.25 inch.[1] The movements of the birds could be traced completely by the tracks which they left in the sand. By means of a small whisk broom these tracks were obliterated after each trial.

It will be seen that the maze offers both a long and a short way to *O*. A few of the birds learned the maze at first by the long way; all adopted the shorter way before the experiment was over.

The maze was placed in a large room, which was well lighted by 2 windows, one to the west of the maze, the other to the north.

Since the birds were perfectly habituated to handling they were placed by hand at *H* and their time in reaching *O*, together with the number of errors made, were recorded by me. Thinking that my presence might influence the reactions of so keen-sighted a bird, I watched their reactions through a small auger-hole bored through the south wall of the room.

Two trials per day were given, one at the morning feeding and one 6 hours later at the noon feeding. The birds were allowed fully to satisfy their hunger after each successful trial in the maze. The night feeding was not made in connection with the maze, but in the large experimental cage which remained out in the open. Four sooties, of which 3 were males, and 3 male noddies learned this maze.

THE BEHAVIOR OF THE SOOTIES IN LEARNING A MAZE.

I began feeding the sooties in the maze by blocking off the runway *G* from the rest of the maze and by closing the entrance to *S*. The cover of the maze was raised and the bird was then put down in this runway and allowed to come out at *O* and walk up the inclined platform to the food which was contained in a dish resting upon a box 8 inches high.[2] Two feedings were sufficient to accustom them completely to this situation, but since the noddies were not sufficiently developed to begin work upon the maze, I fed the sooties in this way for 7 days.

The sooties began learning the maze properly when they were 15 days of age. At this age they are as fully developed, so far as coördination of movement is concerned, as the noddy at 19 days.

Table 3 and the graph (fig. 3) constructed from it show the time-records and the general features of the learning process.

---

[1] This method is fully as accurate and far more cleanly than that of using smoked paper.

[2] See p. 244 for tests on learning to walk up an inclined plane to the top of a box. The same plane and box used there were employed in this connection.

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Fig. 25.

Fig. 26.

Group activity of Terns.

Fig. 25. Noddies attacking a strange bird.

Fig. 26. Peculiar behavior of the Terns when one of their number has fallen into the water. (Neither species swims with any success.)

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TABLE 3.—*Individual and average time-records of four sooties in learning Porter's simple maze, in minutes and decimals of minutes.*

No. of trial.	Bird I.	Bird II.	Bird III.	Bird IV.	Average	No. of trial.	Bird I.	Bird II.	Bird III.	Bird IV	Ave
1	15.00	16.00	16.00	25.00	18.00	18	0.66	0.75	0.83	0.16	0.60
2	20.00	4.00	14.00	5.00	10.75	19	.33	2.21	.38	.20	.70
3	20.00	6.00	13.00	2.00	10.25	20	.33	.61	.96	.30	.55
4	9.00	7.00	10.00	2.78	7.18	21	.21	1.33	.98	.50	.75
5	.83	1.50	14.00	1.33	4.41	22	.30	.88	2.12	.26	.89
6	.83	1.16	2.25	.75	1.24	23	.30	.50	.26	.25	.32
7	2.33	4.80	1.93	1.18	2.56	24	.23	2.16	.56	.36	.82
8	.98	.91	.45	.78	.78	25	.28	.55	.58	.25	.41
9	.98	1.28	1.55	.30	1.02	26	.13	.33	1.50	.26	.55
10	.78	1.25	.61	1.00	.91	27	.26	.58	.81	.20	.46
11	.96	1.05	1.00	1.50	1.12	28	.20	.30	.58	.30	.34
12	1.28	1.35	.46	.95	1.01	29	.58	.73	1.99	.20	.87
13	.36	.33	1.12	.33	.53	30	.26	.30	1.20	.31	.51
14	2.61	.61	.35	.83	1.10	31	.23	.23	.35	.25	.26
15	.68	1.12	.50	.41	.67	32	.21	1.09	.38	.13	.45
16	1.75	1.38	1.05	.33	1.12	33	.20	.30	.58	.23	.32
17	.75	3.00	.55	.23	1.13	34	.23	.25	.31	.16	.24

The error record is practically valueless because of the habits of the birds and of the unsatisfactory nature of the maze.[1]

The general features of the learning process are apparently not very different from those obtained by Porter on the pigeons, English sparrow and other birds. The time of the sooties, however, is markedly longer

[1] I have been criticized both by Yerkes (Jour. of Phil., Psychol., and Scientific Method, vol. IV, p. 585) and by Miss Washburn (Jr. Comp. Neurol. and Psychol., vol. XVII, p. 532) for not presenting the error record in the case of the normal and defective rats which learned the modified Hampton Court maze (John B. Watson: Kinæsthetic and Organic Sensations: Their Rôle in the Reactions of the White Rat to the Maze. Psy. Rev., Mon. Supp. No. 33). I wish to say in this connection that mazes constructed along the lines of these two do not permit of a satisfactory error record without an infinite amount of time being consumed in the process. With the above (Porter) maze a satisfactory error record would have to be made on a basis of the exact number of inches traversed in cul-de-sacs, the number of returns made, the number of false turns made, etc. There would have to be some way of indicating the value of a hesitancy at a blind alley, of a full turn into a blind alley, and the difference in error value between traversing, say, 5 inches in an alley and going its full length, etc. If one attempted to present an accurate record of the errors of a test, one would consume several pages in the description of each of the first few trials. If, on the other hand, one does not present such a descriptive record, and chooses arbitrarily to call any random movement an error, giving all errors equal value, however much the random movements may differ in kind and extent, as Porter (op. cit., p. 253) did in the case of the sparrows, pigeons, etc., and as Kinnaman (Am. Jr. Psy., vol. 13, I, 173–218) did in tests on the monkeys, the record becomes valueless as a basis of comparison with the work of others. Errors in this sense mean nothing except possibly to the man who records them. Our technique in the field of animal psychology is so crude at the present stage of the development of the science that the problems which we present to our animals are not of the kind which easily permit the recording of "errors." I shall welcome as eagerly as anyone a reconstruction of the field in such a way as to permit such records. (Since writing the above I have succeeded in devising a satisfactory method for testing animals in the maze which permits us to give both the time record of each trip and a record of the *total distance traversed* by the animal at each trip.)

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than is the case with the birds observed by Porter. The reason for this is quite clear when one recalls that the sooties will stand perfectly still sometimes for an hour or more. Most of the time consumed by the birds was spent in idling at *H* or in standing in some other part of the maze. I have compared my record of "errors" with that given by Porter, and find that if anything the number of errors made by the terns is less than

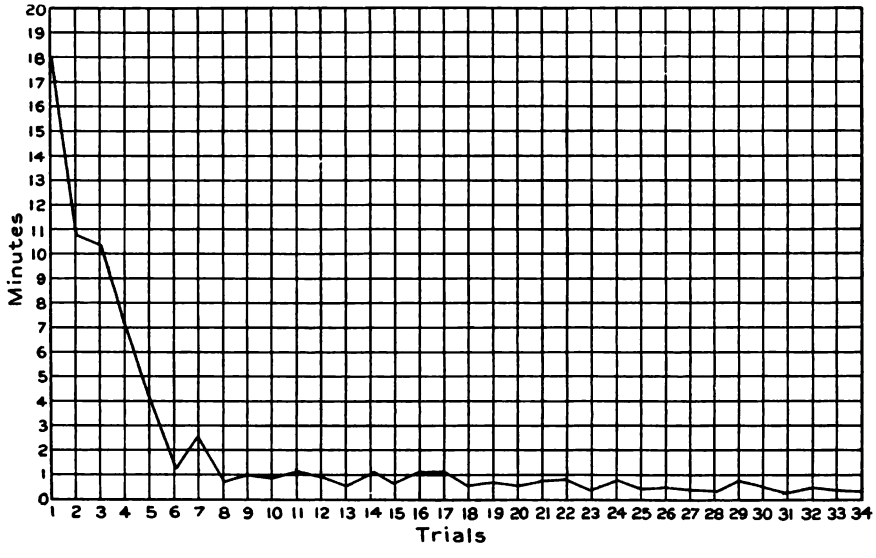

FIG. 3.—Curve showing average time of four sooties in leaving Porter's simple maze.

that made by many of Porter's birds. Porter records 3.5 errors for the vesper sparrow; 91 errors for the cowbird; 7.5 for English sparrow F 5; 58 to 45 errors for English sparrow M 6; 121 errors for English sparrow F 7; and 11 errors for English sparrow M 8, as being the total number of errors made by his birds in their first two trials.[1] It would be absolutely impossible for the young terns, with their idling habits, to make, within the time-limit shown above, anything like the number of errors which some of Porter's birds made in the time shown in their records.

If the time for idling, which is a characteristic mode of behavior and is not due to a lack of hunger, were taken out the curve as shown above would be much smoother and would lie very much nearer to the base line. If the latter part of this curve be compared with the corresponding portion of a similar curve obtained from the rat in learning the Hampton Court maze,[2] its extreme irregularity as compared with the rats' curve will at once become noticeable. The terns never become the automata which the rats

[1] What do "errors" mean in such cases as these!
[2] Watson, J. B. Op. cit., p. 100, curve III.

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become. The jerky, uneven reactions of the adult sooty are already showing themselves in the early behavior of the young sooty.

THE BEHAVIOR OF THE NODDIES IN LEARNING A MAZE.

The same routine of learning the maze was adopted in the case of the noddies as was described above for the sooties. The noddies, however, were 19 days of age before they were comparable as regards development with the sooties, 15 days of age.

Table 4 and the graph constructed from it (fig. 4) show the time-records and the characteristic features of the formation of this association.

TABLE 4.—*Individual and average time records of three noddies in learning Porter's simple maze in minutes and decimals of minutes.*

No. of trial.	Bird I.	Bird II.	Bird III.	Average.	No. of trial.	Bird I.	Bird II.	Bird III.	Average.
1	16.00	7.00	8.00	10.33	13	0.43	2.12	0.18	0.91
2	17.00	7.50	9.00	11.16	14	.41	.20	.28	.29
3	19.00	.83	22.00	13.94	15	.43	.33	.43	.39
4	7.00	3.00	6.00	5.33	16	.46	.33	.33	.37
5	7.00	5.00	3.00	5.00	17	.25	.45	.28	.32
6	7.50	.66	2.25	3.47	18	.81	.60	.30	.57
7	3.50	7.50	.95	3.98	19	.33	.33	.16	.27
8	7.00	2.00	1.00	3.33	20	.30	.33	.30	.31
9	8.50	4.00	1.50	4.66	21	.33	.45	.20	.32
10	3.00	5.00	1.00	3.00	22	.25	.58	.46	.43
11	.73	4.00	3.00	2.57	23	.38	.51	.33	.41
12	1.93	.83	2.16	1.04	24	.33	.55	.25	.37

The noddy is very much slower in learning the maze than the sooty: (1) because of less general activity, and (2) because of longer periods of standing. Mention has already been made of the habit of the adult noddies of standing motionless for hours upon the top of any object which projects from the surface of the water. When the young noddy is placed at the unfamiliar position at *H*, he shows the tendency to react in this way to a marked degree. Although I exerted every care to keep the food conditions constant, I found that the first few trials of the noddy were quite unsatisfactory. So persistently would they stand in their tracks at *H* that I finally had to arouse them by tapping on the wall. The first three trials recorded above are valueless for this reason. From the fourth trial on, however, the records were made in the usual way. The errors are not markedly different in point of numbers or in kind from those of the sooty. The above curve, with the limitation above noted, is quite characteristic. It will be observed that 13 trials were necessary to bring the curve down to the point representing one minute of time. This point was reached by the sooty at the eighth trial. This brings out the general fact which I have noted elsewhere,[1] that the young sooty is much more active than the young noddy.

[1] See p. 243.

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In any given problem, the successful solution of which depends upon random activity, the animal which has the greatest activity is likely to show a shorter time record for the early trials.

In the second place, the curve for the noddy drops to a minimum at the fourteenth trial, which is maintained almost uniformly for the rest of the tests. The variation occurring throughout the curve for the sooty has already been remarked upon. A comparison of the two curves from the fourteenth

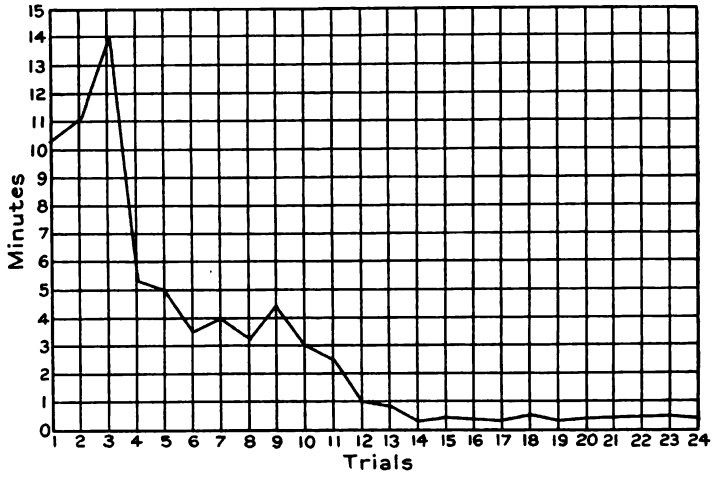

FIG. 4.—Curves showing average time of three noddies in leaving Porter's simple maze.

trial on brings out what I consider the second great difference between the two species: The sooty is highly excitable and nervous; the noddy is stolid and indifferent. The sooty, even though going through habitual reactions, is disturbed by slight changes in intra and extra-organic stimulations; the noddy on the other hand is indifferent to slight changes in stimulation.

While these conclusions are based, it is true, upon few records, I feel after much observation of the birds that the amassing of a larger number of statistics would establish even more firmly the conclusions given above.

EXPERIMENTS WITH THE MAZE IN FAINT ILLUMINATION AND IN TOTAL(?) DARKNESS.

The trained animals used in the above experiment were tested at night with the maze faintly illuminated. The situation was as follows: For two or three days I had accustomed the birds to a late night feeding. I then made the room in which the maze was kept completely dark by boarding up the windows. I next mounted a commercial candle of ordinary size (standard candles were not available) upon a glass plate. I then suspended the candle so mounted over the center of the maze at a height of 50 cm. I found it absolutely impossible under these conditions to avoid shadows

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Fig. 27.

Fig. 28.

Group activity of Noddies. Sunning reaction.

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being cast over many of the pathways; consequently the results are more or less vitiated by this circumstance. I determined, however, to test the birds under these conditions. The birds were kept in the room for 45 minutes before being tested in the maze. They were quite lively and hungry. All other conditions of the test were the same as in daylight. The behavior of the sooties is shown in the following:

Sooty I: Started the short way as usual, but the deep shadows seemed to deter him. Turned into E and came to O by the longer route. Time: 1.50 minutes.

Sooty II: Bird ran quickly completely around H. Came out and ran rapidly to L. Was deterred as in above case, ran into I and on into Z, came back to L and ran the full length of L and M and then went out the short way through S to O. Time: 2.66 minutes.

Sooty III: Ran out rapidly from H into I and then into Z, then turned and went into R and then into E and ran up and down the alley R and E three times. On the last trip passed on through F and G to O. Time: 2.80 minutes.

Sooty IV (female): This bird behaved very peculiarly. She spent 15 minutes in H. Came rapidly out to L, turned in there and ran the full length of M, came back and ran up I into Z, then back down I and poked head into R. Shadows there apparently disturbed her and she turned back into L. Dug a little hole there in the sand and after standing furtive and alert for 10 minutes, went to sleep. Total time under observation: 45 minutes. No success.

It is perfectly clear from the above test that the birds can run the maze in a faint light. Whether they can run it without error in the given illumination can not be decided until we can eliminate the shadows which were mentioned above.

On account of the unsatisfactory nature of this test the noddies were not tried in the same way.

The next night I tried the birds with the maze in total darkness. The birds were carried in as usual and left in the maze room for half an hour before being tested. An electric contact and signal had been arranged to warn me when the bird stepped upon the inclined plane at *O*. Great care was taken to remove all tracings from the sand so as to get a complete record of the trial movements of the birds.

The results of this test are curious. Each bird was left in the maze at its respective trial for 30 minutes. No signal reaching me, I then went in with my lantern. Not a single bird had moved from its tracks. Each had stood motionless at the point in *H* at which I had set him down. As soon as light was brought into the room the bird began "peeping" and moving.

It is clear from these tests that the light *conditions activity* in these

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birds.[1] Under natural conditions in the field they are never in total darkness. Starlight on the island is exceedingly bright. We can not conclude from this test, however, without additional control tests (which I had no time to make), that the terns run the maze wholly by means of visual data or that they even learn it wholly in terms of visual data.

EXPERIMENTS UPON THE ROTATED MAZE.

One test was made upon the maze after it had been rotated 90 degrees to the north. The birds, for example, instead of traversing *S–O* in a southerly direction, must now traverse this alley in an easterly one. The relations of the turns, however, were not altered by this change; only the cardinal directions were altered. On account of my having to leave the island, much to my sorrow, on the following day, this experiment could not be extended to the other directions. The results of this test were as follows:

SOOTY IV.

First trial: Bird acted very peculiarly at H. Came out of H, but ran tion L. Became confused, went up I, then into F and on around the long way. Time: 0.91 minute. (Normal time for control test: 25 minutes.)

Second trial: Bird badly confused. Ran full length of L, then up I, then full length of Z, back down I, turned into R, then went long way via E, F, and G. Time: 2.43 minutes.

SOOTY III.

First trial: Perfect. Time: 0.20 minute.

Second trial: Stumbles about at H, making circus motions, apparently trying to find entrance. Becomes discouraged, goes into L and runs full length. Comes out and runs up I. Into F, then to O by long route. When he reaches the east corner of the maze, he stops and tries to poke head out through the meshes of the wire. This direction had formerly led to the food. Time: 2.75 minutes.

A third trial was given the following morning. Bird ran round to S, became confused, turned into E and came to O by long route. Time: 0.81 minute.

SOOTY II.

First trial: No error. Time: 0.31 minute.

Second trial: Bird badly confused. Ran full length of L. Came out, turned into S. Movements hesitating and slow. Time: 0.75 minute.

SOOTY I.

First trial: Perfect. Time: 0.20 minute.

Second trial: Bird badly confused. Every error in the maze was made again and again. Finally reached O by the long way. Time: 2.91 minutes.

[1] Both species were tested to see if they would feed (without aid from me) in a photographic dark-room. The test was very carefully made. Neither the noddies nor the sooties would stir from their tracks. All sounds were hushed. The sooties would no longer reply to my "peep" as they would customarily in starlight.

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Third trial: Given this bird on the early morning of the following day. No full errors were made, but the bird showed a clearly marked tendency to turn in the old direction. Time: 0.25 minute.

NODDY I.

First trial: Perfect. Time: 0.16 minute.

Second trial: Is confused and hesitant. Tries at two points to turn in the old direction. Time: 0.43 minute.

NODDY II.

First trial: Hesitancies, but no error. Time: 0.41 minute.

Second trial: Confusion evident. Tendency to turn in the old direction very marked. Time: 0.56 minute.

NODDY III.

First trial: Badly confused at H. Tries in vain at first to find the exit from H. Runs full length of L, then out and up I into F and comes to O by long way. Time: 0.91 minute.

Second trial: Runs full length of L, starts to run into S, but withdraws head, turns and goes up I, turns into Z and goes full length, comes back down I, runs into R, turns and goes up E on wrong way to O. Time: 2.43 minutes.

From these experiments we are justified, I think, in concluding that there are some data used by these birds in this reaction which are not clarified by applying the term "visual" to them.[1] Porter's results on the English sparrows and other birds, obtained by testing trained birds in the reversed maze, are very similar to the ones reported here. My own experiments on normal, blind, and anosmic rats when tested in a similar way gave results which corroborate the above.[2]

An explanation of the disturbances in the reactions of the birds which ensue upon changes in the directions of the alleys of the maze can not be made until a more complete and better controlled method of experimentation is at hand.

[1] There are two possible sources of error in this experiment. In the first place, the "environment" was not rotated with the maze; in the second place, the rotating of the maze changes its position with respect to the two sources of light. Owing to the conditions under which I worked, I could not control these defects. Porter in his work on the reversed maze (op. cit., p. 256) makes no mention of either of these two possibilities of error.

[2] Op. cit., p. 86.

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IX. AN EXPERIMENTAL FIELD-STUDY OF WARNING COLORATION IN CORAL-REEF FISHES.

By JACOB REIGHARD,
Professor of Zoology in the University of Michigan.

5 plates.

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AN EXPERIMENTAL FIELD-STUDY OF WARNING COLORATION IN CORAL-REEF FISHES.[1]

By Jacob Reighard.

I. INTRODUCTION.

The islands of the Tortugas group rise gently from a submerged plateau many square miles in extent. To the southeast, at a distance of about 3 miles, is the outer reef, and beyond this deep water. Immediately about the islands the bottom is overlaid by the gray-white or yellow-white coral sand and, except where traversed by the few tortuous channels, it is covered with water from 8 to 15 or 20 feet in depth. From this bottom the inner reefs rise sheer. These vary in size from isolated coral heads of a square yard or two in area to small reefs of a few square rods or a fraction of an acre. The upper surfaces of these reefs are sometimes exposed at low tide, and at all tides one may readily wade over them. (See plates in Saville-Kent, 1893, of the Great Barrier Reef of Australia.) Although nearly level on top, the reefs are penetrated in every direction by chasms, fissures, and tortuous covered passages which intercommunicate so as to form veritable labyrinths. Structurally the whole is not unlike a mass of small boulders carelessly piled and roughly cemented together (plate 1; plate 2, fig. 3; plate 4, fig. 8). On its upper surface and for a short distance downward into the larger fissures each reef is clothed with living coral, massive or branched; beneath this is dead coral and coral rock.

The crevasses of the coral reefs harbor many species of teleostean fishes. The smaller species and the younger individuals of the larger species are never seen at a distance from this shelter. On the reef and in its immediate neighborhood they find their food; when disturbed they scurry to the reef and vanish into its protecting mazes. As the disturbance subsides they slowly emerge, in the inverse order of their timidity, and gradually resume their wonted activities.

The larger individuals of those species that reach a considerable size may wander from the reef to a distance of some rods, protected from piscivorous fish of their own size apparently by their bulk. Thus *Abudefduf*

[1] Contributions from the Zoological Laboratory of the University of Michigan, No. 116.

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and *Hepatus* may reach the shore and mingle there temporarily with the colonies of predaceous gray snappers. They invariably return in a short time to the reefs.

The colors of the reefs themselves are subdued. The coral rock is gray, in places nearly white. The mantle of coral polyps seen in mass varies from cream to light-brown or delicate pea-green. It is almost a monochrome. Only the dark shadows in the fissures or an occasional purple sea-fan lends contrast to the picture.

The coral-reef fish are nearly all conspicuous (plates 1 to 5, except fig. 9) either because of bright colors, patterns of contrasting colors, bizarre form, erratic movements, or because of some combination of these qualities. They often combine with conspicuousness disagreeable qualities in the form of defensive spines. The characters of some of these fish are given in table 13, page 299, and are discussed in section VIII of this paper. The conspicuousness is that commonly found in insects said to be warningly colored and the combination of this with defensive spines suggests the combination of conspicuousness and disagreeable qualities of many warningly colored insects.

In contrast to the fishes of the reefs are those commonly seen over the bottom of coral sand near shore. These are inconspicuous. The gray snapper, *Lutianus griseus,* as it appears over the coral sand (plate 4, fig. 9), is an example. It is piscivorous and its close agreement in color with its environment appears to be a case of *general aggressive resemblance.* Its common prey during my stay at the islands was the so-called sardine or hard-head, *Atherina laticeps.* This also is inconspicuous. It is almost invisible when seen from below against the surface film, as it ordinarily appears to the gray snapper. The fish is a plankton feeder. It does not find its food on the reefs nor seek their shelter. Its color is an instance, apparently, of *general protective resemblance.* Photographs were obtained of this species in its natural environment. Although the photographs were excellent the fish were so inconspicuous that the loss of contrast in the pictures, inevitable in the process of reproduction, made it inadvisable to make plates from them, as they would have shown practically nothing.

II. THE PROBLEM STATED.

The conspicuousness of coral-reef fish appears to me to exclude any explanation based on protective or aggressive resemblance (*cf.* Wallace, 1891, p. 266). Semper (1879, p. 386) says, speaking apparently of coral reefs in general:

> The surface of a reef lying just under water has often been compared to a gay garden of flowers and the splendour of such a "bed" of animals is in fact quite astonishing. It is as though mother nature had here given free play to the fancy she is elsewhere compelled to restrain in some degree, by indulging her delight in lavishing all the colors of the rainbow and by inviting a motley company of creatures to disport themselves among the flowers and fruits of her submarine garden—blue and red star-fish, Holothuriæ, of every hue, and gaudily painted fishes.

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The gaudily-painted fish occur on the inner reefs of the Tortugas, but the "brilliant colors of the rainbow," "the flowers and fruit" I am unable to see in their environment. The brilliant fish are therefore conspicuous against a dull and nearly uniform background. I know of nothing in the environment which they resemble even remotely.

Striking sexual differences have not been noted in these fishes by systematists, and I have observed none. I am unable to tell the sex by any external character. Sexual selection seems therefore to be excluded as a possible explanation, although it is to be expected that when we know the mating habits of the fish we shall find that they include displays of color.

The theory of warning color often applied to certain of these fishes, most recently by Bristol (1903), seems then to afford the most plausible explanation of their conspicuousness. This theory attempts to account for conspicuousness, more particularly in insects, by its association with some disagreeable quality. The vertebrate enemies of the conspicuously colored animal are believed to be warned of its disagreeableness by its color. They thus learn to avoid it. In this way, in each generation, the most conspicuous are preserved and through this selection conspicuous coloration is believed to have been perfected. The theory thus attaches to warning coloration a biological significance—a present function—while at the same time it affords an historical explanation of the coloration, by asserting that it has been perfected through past selection of the functionally best adapted.

The present paper embodies the results of a search for the biological function of the brilliant colors and striking color-patterns of conspicuous coral-reef fishes. If it appear that a warning function does not at present attach to this conspicuousness, then it becomes extremely improbable that it could have arisen in connection with such a function.

The theory of warning colors embodies certain fundamental assumptions which it seemed possible, in the particular case in hand, to test experimentally.

(*a*) As stated by Beddard (1892, p. 155), "The theory of warning color implies not a special recollection of any type of insect, but a general association of bright colors with poisonous or dangerous qualities." A like idea is expressed by Poulton (1887). After pointing out the few colors and limited number of patterns among warningly-colored insects, he says: "It is to be noted that advantage would accrue in the greater thoroughness of the education, no less than by shortening the process, for a few colors with a few simple patterns would be remembered more easily than a larger number with a separate pattern in nearly every species." Again, following Meldola (1882), he says: "All the conspicuous and dangerous or distasteful species in any country will be found to share between them a few strongly contrasted colors, arranged in few and simple patterns again and again repeated."

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(*b*) The theory of warning color assumes that the enemies of warningly-colored species are capable of discriminating colors.

(*c*) The theory assumes that the enemies of warningly-colored species are able to form associations between the conspicuous colors and patterns of their prey and their disagreeable qualities.

(*d*) The theory assumes that the associations thus formed between conspicuousness and disagreeable qualities are indefinitely retained (associative memory).

It seemed possible to test these four assumptions by experiments on the predaceous fish that occur about the coral reefs or along the nearby shore. Do certain colors in themselves convey a warning so that prey showing these colors is avoided? Have the predaceous fish color vision? Do they form associations? Have they associative memory? Experimental evidence on these points is presented in sections IV, V, and VI of this paper.

Should the predaceous fish be found to have the qualities assumed by the theory, the warning color explanation of the conspicuousness of coral-reef fishes becomes more probable. But it would still need to be learned by feeding experiments whether any of the species of conspicuous fish are avoided, whether any show that combination of conspicuousness with qualities sufficiently disagreeable to render them relatively free from the attacks of predaceous fish under the conditions that normally prevail. Experiments involving the feeding of conspicuous coral-reef fish to predaceous forms are described in section VII.

Through the courtesy of Dr. A. G. Mayer, Director of the Marine Biological Station of the Carnegie Institution of Washington, I have been able to spend parts of the months of June and July at the station during the seasons of 1905 and 1907, while acting as assistant of the U. S. Bureau of Fisheries. I am indebted to the U. S. Fish Commissioner, the Hon. George M. Bowers, for permission to publish the results of my work.

III. GENERAL METHOD EMPLOYED.

The gray snapper, *Lutianus griseus* (Linnæus), was chosen as the subject of the experiments. This, the commonest predaceous fish of the region, averages 12 to 15 inches in length. At the Tortugas it is found about the inner reefs, but occurs also along the shore of Loggerhead Key wherever there is shelter. Nearly all of the individuals along the shore were, during my stay, aggregated in three colonies. The largest of these colonies was under the Laboratory dock and consisted in the summer of 1907 of from 150 to 175 individuals, but was smaller in 1905. The two other colonies were found under the two docks belonging to the lighthouse, one on the east side of the island and the other on the west. Each was about a quarter of a mile distant from the Laboratory colony. The personnel of each of these colonies seemed to be fairly constant. During the day individuals rarely

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Fig. 1. Rock ledges near beach, showing three *Abudefduf marginatus* banded with black and yellow-white, and two grunts (*Hæmulon sp.*, probably *sciurus*) striped with blue and yellow.

Fig. 2. *Abudefduf marginatus* in crevasses of a reef of massive coral, *Orbicella*. Note mantle of living coral polyps.

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wandered more than a short distance from the dock and always returned to it. I do not of course know that no changes took place in the colonies at night, but the results of the experiments as detailed below indicate that such changes must have been few.

The gray snapper feeds in the daytime and by sight. It usually approaches its prey slowly from below. When near enough (1 to 3 feet) it strikes quickly and, judging its distance with great accuracy, seizes the food, turns sharply, and returns to near its starting-point. The whole movement greatly resembles that of the end of a whip-lash when the whip is cracked; hence probably the name " snapper." The fish were entirely at liberty during the experiments and were taking their normal food and leading their normal life in an unmodified environment. The Laboratory colony was habituated to the frequent presence of people on the dock and paid little heed to them so long as they did not approach nearer than about 15 feet. This colony occasionally received food thrown from the dock and the fish were then accustomed to assemble, but the food received in this way was not enough to affect their normal appetite. They were always hungry. This feeding was, moreover, discontinued during the period covered by the more important experiments. That it did not affect the experiments appears from the fact that the fish at the other docks were not fed, and yet their behavior was identical.

The commonest food of the gray snapper in June and early July is the so-called sardine or hard-head (*Atherina laticeps*), a silvery-white fish about 2 inches long. It occurs in immense schools along the shore and is constantly pursued by gray snappers. To test the power of the gray snappers to discriminate colors, from associations, and retain them, atherinas were dyed various colors, as described below, and thrown from the dock to the snappers. The experiments were therefore mass experiments, in which an entire colony of gray snappers participated without being removed from their accustomed habitat.

The water is very clear at the Tortugas, and it is usually calm on one side or the other of the island, so that the observer on the dock sees the snappers clearly and is able to record the results of an experiment without difficulty.

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IV. REACTION OF THE GRAY SNAPPER TOWARD ATHERINAS TO WHICH HAS BEEN GIVEN WARNING COLORS AND TOWARD THOSE OF ABNORMAL FORM, ODOR, OR TASTE.

ABNORMAL COLOR.

As the atherinas used in the feeding experiments had usually been colored by an aniline dye and were therefore dead, a test was first made of the reactions of the snappers toward dead and living atherinas. After a single normal uncolored atherina had been thrown to assemble the snappers, 18 other normal atherinas were thrown dead and living alternately. One was taken as quickly as the other. In no case was there any observable hesitation in making the first snap at either dead or living fish.

TABLE 1.—*Results of feeding gray snappers of the laboratory colony on "warningly-colored" atherinas in July, 1905.*

Exp. No.	No. of atherinas fed.	Color.	Method of staining.	Results.
1	6	Bright vermilion.	Diamond package dye fast scarlet, 5 minutes; weak acetic acid, 2 minutes.	Thrown in succession. All taken, No. 1 at once, while experimenter was 15 feet distant. Nos. 2 to 6 with hesitation while he was but 6 feet distant.
2	7	Deep vermilion.	As under 1, but stained 10 minutes.	Thrown alternately with normal fish from distance of 15 feet. All taken instantly.
3	7	Deep vermilion.	As in 2.....	As in 2.
4	7	Yellow.....	Stained 20 minutes in saturated solution of picric acid in sea-water and then rinsed.	Thrown alternately with normal fish, from a distance of 15 feet. All taken instantly.
5	8	Green	Stained in weak methylene-blue and then in picric acid.	Thrown consecutively, from distance of 15 feet. All taken as quickly as normal fish.
6	7	Dark blue ...	Stained in methylene-blue in sweet water, then rinsed in sea-water.	Thrown alternately with normal fish from a distance of 15 feet. All taken at once.
7	7	Dark blue ...	As under 6.	Thrown consecutively from a distance of 15 feet. All taken at once.
8	7	Sky blue.....	As under 6, but for a shorter time.	As under 6.
9	7	Sky blue.....	As under 8.....	Thrown consecutively from a distance of 15 feet. All taken at once.
10	17	Brilliant purple.	Diamond package dye violet, used as in experiment 1.	Thrown alternately with normal fish from a distance of 15 feet. All taken instantly.

Atherinas were then given various colors by staining them as shown in table 1. These were thrown to snappers with the results shown in the table. It appears from the table that the snappers take atherinas colored bright vermilion, deep vermilion, yellow, green, dark blue, light blue, and purple, and all without hesitation and as readily as they take normal or uncolored fish.

Not only were fish of all colors taken at once, but they were taken as readily when offered in succession as when offered alternately with normal fish. The snappers showed no hesitation in taking atherinas of any of the

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colors used, except when the experimenter was too near them. Thus in the first experiment the first red fish thrown from a distance of 15 feet was taken at once, while the remaining 5 thrown when the experimenter was only 6 feet from the snappers were taken with some hesitation. In subsequent experiments the experimenter did not approach nearer than 15 feet and the colored atherinas were then taken readily. In only a few individual instances was any hesitation observed, and it was then found that this was coincident with the moving about of some person on the dock and that it concerned uncolored fish as well as colored. It is an interesting fact that this hesitation is greater if someone is fishing from the dock with a rod.

The colors used ranged through the spectrum, although none of them, so far as I know, is a pure spectral color. Since the snappers gave no evidence that any of these colors served to warn them, it becomes highly improbable that any color in itself has a warning meaning to them. Had any color had such meaning they should have refused it or taken it with great hesitation. This conclusion seems to me warranted, even though the food offered them is, except for its color, one which they take at this season with great frequency.

ABNORMAL TASTE OR ODOR.

In order to study in a preliminary way the behavior of the snappers toward substances of disagreeable odor or taste, atherinas stained red were treated with various substances and thrown to the snappers with the results

TABLE 2.—*Reactions of Laboratory colony of gray snappers toward atherinas treated with substances having unpleasant odor or taste, July, 1905.*

Exp. No.	No. of atherinas.	Substance used.	How prepared.	Results.
11	10	Formic acid 9 per cent.	Stained in fast scarlet containing 9 per cent formic acid; rinsed in sea-water.	Thrown after 3 red fish not treated with formic acid; some hesitation over first 2 of these. All formic reds taken at once.
12	8	Formaldehyde 40 per cent.	Red fish eviscerated and body cavities filled with absorbent cotton, which was then saturated with formaldehyde.	Thrown after 3 normal fish; all taken at once; none seen to be rejected.
13	10	Formaldehyde 40 per cent.	As in 12, but surface of body also wet with formaldehyde.	As in 12; all taken at once; 1 formalin red swallowed with some hesitation.
14	10	Red pepper..	Red fish wiped dry, smeared with vaseline, rolled in red pepper; very hot to tongue.	Thrown after 3 plain reds; taken at once; one swallowed slowly.
15	10	Quinine	Prepared as in 14, but with quinine; very bitter to tongue.	Thrown after 3 normal fish; all taken at once.
16	10	Red pepper and quinine:	As in 14, but with mixture of red pepper and quinine.	As in 15.
17	15	Red pepper, quinine and formic acid.	Prepared as in 11, then as in 16.	As in 15.
18	10	Ammonia fortior.	Red fish wet with ammonia fortior.	As in 15.
19	10	Carbon disulphide.	Red fish thrown directly from bath of carbon disulphide.	As in 15.

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shown in table 2. To call together the snappers 3 atherinas were thrown at the beginning of each experiment. These were either normal or stained red, but were not rendered disagreeable. The first 2 of these (experiment 11) were taken with some hesitation, but all other atherinas offered in the nine experiments were taken as readily as normal fish. If any of them had been subsequently rejected their red color would have made them conspicuous objects on the sand bottom. None were seen to be rejected. In two cases the fish, after being taken, were swallowed slowly. They could be seen protruding from the mouth of the captor, which, pursued by other snappers, slowly swallowed them. The substances used are as disagreeable to man as any that I know, some by reason of their taste, others on account of their odor or because they act as irritants. Probably none of them occur normally in the environment of the snapper.

ABNORMAL FORM.

To test the behavior of the snappers toward food of abnormal form, normal atherinas were modified in form as shown in experiments 20 to 25.

Experiment 20: By removing the body between the anal and pectoral fins and sewing together the head and tail so as to produce a very much shortened form.

Experiment 21: By removing the heads of two individuals and sewing the bodies together end to end so as to produce a very much elongated fish with a tail at each end.

Experiment 22: By sewing together the bodies of three fish after removal of the heads and tails and thus forming a flat rectangular piece.

Each of the modified forms was thrown to the snappers separately after a number of normal atherinas had been thrown to assemble them. The first (experiment 20) was taken with a little hesitation, but the rest were taken as readily as the normal fish. Separate heads and separate tails of atherinas were taken with the same readiness.

Experiment 23: A piece of white twine 12 inches long and about 0.04 of an inch in diameter was tied by one end about the head of an atherina. It was thrown after one normal fish and taken at once.

Experiment 24: A brown cord about 15 inches long and a sixth of an inch in diameter was tied by one end about the head of an atherina. This was thrown after a single normal atherina. There was a moment's hesitation, three snaps which fell short, and then the fish and cord were taken.

Experiment 25: An atherina was wrapped in cheesecloth and this rubbed with another atherina. It was thrown after a single normal atherina and was at once taken and was not seen to be rejected.

From the preceding experiments it appears that modifications in the color, form, and chemical properties of the normal food do not prevent the gray snapper from taking it. The number of snappers involved in the experiments is so great that it is improbable that any individual had more

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than a single experience with any one sort of modified atherina. The evidence, therefore, does not show that the snappers do not learn by experience; it shows merely that they try every new possible-food object that comes into the environment. This fact that the behavior of the snappers has yet to be adjusted to each particular kind of new food is itself of importance in connection with the theories of warning color and mimicry. The snappers have, for instance, formed no habit of rejecting food of a particular color. So far as concerns new possible-food they are still in the condition of the young chick which pecks at all sorts of small, near objects. That the behavior of the snapper may be rapidly adjusted to new qualities in its food appears in a later section of this paper. The necessity of such constant food adjustments is clear when we remember that the snapper increases many thousand-fold in bulk in its growth from the egg to the adult condition. Between the minute forms which must serve as the food of the very young fish and the larger forms upon which the piscivorous adults feed there is a wide gap, which must be bridged in the food of the growing individual. In the process of adjustment of the individual snapper a warning-color reaction may conceivably be established and may then be utilized by a mimicking form.

V. COLOR DISCRIMINATION IN THE GRAY SNAPPER.

EXPERIMENTAL METHODS EMPLOYED.

It has been shown (table 1) that gray snappers take without hesitation red, yellow, green, blue, and purple atherinas, one with as much readiness as another. There is thus suggested the possibility that these fish may be unable to discriminate colors,[1] an inability which would, if common to the predaceous fish of the reefs, be fatal to the theory of warning coloration. To test the color-vision of the gray snapper the laboratory colony was fed on dead atherinas that had been artificially colored. The natural silver-white color of the atherinas and the almost complete lack of pigment in the dermis makes it easy to dye them of a nearly uniform color. In addition to the normal white atherinas there were used red, yellow, blue, and green fish of light and dark shades.

The snappers were first fed on atherinas of one color until they had become familiar with that color and were then offered a choice between that color and another and unfamiliar color. Choice was offered by throwing 10 atherinas together from the dock to the assembled snappers, 5 of the familiar color and 5 of an unfamiliar color. The order in which they were taken was recorded, so as to learn whether the snappers showed power of color discrimination by taking first the fish of the familiar color and last those of the unfamiliar color. Each throw of 10 atherinas is called

[1] At the time these experiments were begun I knew of no experimental evidence that fish distinguish colors. Since then Washburn and Bentley (1906) have published an account of experiments on the minnow *Semotilus atromaculatus*, which appears to show color discrimination in a single individual of this species.

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a trial; each experiment consists of a number of successive trials, often divided into several series.

In the preliminary trials the atherinas were taken so rapidly that it was impossible to keep an accurate record. It became further evident that normally hungry snappers might distinguish food of different colors, but might yet, on account of their hunger, fail to discriminate between one color and another. To reduce the rate of feeding to such a point that an accurate record could be kept and to make evident a possible power of color discrimination, it became necessary to prolong the preliminary feeding until the appetite of the snappers had been sufficiently dulled. The number of fresh atherinas taken by a colony of about 100 snappers was usually about 100 during the first minute. The preliminary feeding was continued until this rate had been reduced to 15 or 20 per minute. The discrimination experiments followed immediately thereafter. When, as in 1907, the atherinas used in the experiments had been preserved in formalin they were taken more slowly; the preliminary feeding was then not so long continued and the discrimination experiments began as soon as the rate of feeding of the snappers was slow enough to permit an accurate record to be made.

The atherinas used in each discrimination experiment were of the same average size. Those of the two colors were given a like taste by treatment with acetic acid or formalin as described below. Thus errors due to size or chemical properties are believed to have been eliminated.

In each trial the 10 fish were taken together in the hand and thrown by a single movement of the arm so that they fell upon the water spread over an area of 1 or 2 square yards and intermingled at random. They were seized by the snappers from beneath. The random intermingling of the two colors in each trial, unlike in successive trials, is believed to have eliminated errors of position in the horizontal plane. In the experiments of 1907 all atherinas used were made to float (except in experiment 26, *q. v.*), so that all lay on the water in one plane. Fish which sink are brought nearer to the snappers and are taken more readily than those which float. Thus if the atherinas of one color should sink more readily than those of the other color there would be introduced an error of vertical position. This is avoided by making all the atherinas float, so that all are equally accessible to the snappers.

COLOR DISCRIMINATION EXPERIMENTS (1907).

While *Atherina* was abundant at the Tortugas in June of each year of my stay, it became scarce in July. On my arrival on July 8, 1907, the fish were already so scarce that it was impossible to obtain on any one day the large number needed to conduct discrimination experiments with fresh fish. I had, therefore, to accumulate a supply of atherinas by preserving in formalin those obtained each day. The discrimination experiments (except experi-

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ment 26) were conducted with these preserved fish. After the formalin had been as far as possible removed from them by soaking them in fresh water they were dyed and used precisely as though they had been fresh. The snappers took the formalin fish at first greedily, but after a little experience their rate of taking them became gradually much slower than with fresh fish. This rendered it possible to make a more accurate record of observations, while at the same time it greatly reduced the number of atherinas necessary for the preliminary feeding.

In all the experiments of 1907 the record was made by means of the following device: Two blocks of wood, each 8 inches long, 2 inches wide, and 1 inch thick are held with their broader faces together by a metal pin at each end. This pin is firmly fixed in the lower block, but is received into a hole bored in the upper block, so that the blocks may be readily separated. Through the upper block are bored two parallel rows of holes, 10 in each row, and these holes are continued for about 0.125 inch into the lower block. Into each hole is loosely fitted a flat-headed copper nail an inch and a half long, which is filed round and brought to a blunt, conical point. The observer places one end of a sheet of commercial note paper between the blocks, so that the points of the nails rest on its upper surface. If he is observing the order in which red and blue fish are being taken in a trial of 10 fish, the upper row of nails (nearer the end of the paper) may represent the red, and the lower row the blue. The device is operated by touch, so that the experimenter may watch the experiment while making the record. Beginning at the left, he perforates the paper by pushing down a nail in the upper row when a red fish is taken, a nail in the lower row when a blue fish is taken. After pushing down any nail he shifts his hand one nail to the right. When a record of one trial has been made, those of several succeeding trials are made on the same sheet by separating the blocks and shifting the paper. If the records of successive trials are kept in alignment vertically the vertical columns may be footed for each order and each color. A reduced transcript of such a sheet is given in figure 1, which shows a series of 4 trials with light red and blue. The record of each trial is to be read from left to right. In the first trial the first fish to be taken was red, the next 5 were blue, and the last 4 red. The totals at the bottom of the sheet show in how many of the 4 trials red and blue fish were first taken, second taken, etc. The numbers are the footings of the vertical columns for each color. Thus in 3 of the 4 trials blue fish were taken in the first order or place and in the other red was taken in first order or place. On the other hand, red was taken in the last place in all 4 trials.

Experiment 26: Blue and white color discrimination.—The fresh atherinas were divided into two equal lots. One of these was placed for 20 minutes in a saturated solution of methylene-blue in 0.4 per cent glacial acetic acid; the other lot was placed for an equal time in 0.4 per cent solution

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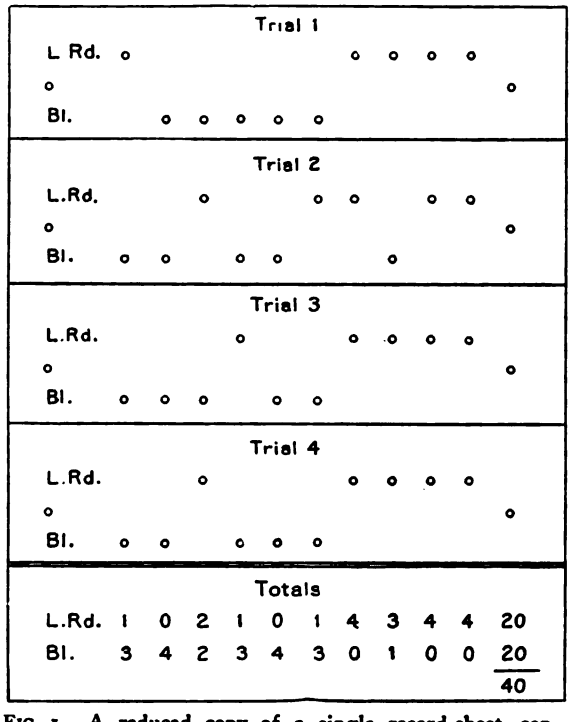
of acetic acid without the methylene-blue. Fresh solutions were used for each experiment. The fish when taken from the solution were quickly rinsed in sea-water, and all had then the same sour taste. Before beginning the experiment the snappers were given a preliminary feeding of normal atherinas until their rate of taking them had been reduced to between 10 and 20 per minute. The discrimination experiment was begun immediately thereafter.



5 light-red atherinas and 5 blue atherinas were thrown in each trial, so that the four trials included 40 fish, 20 of each color. The circles at extreme right and left of the sheet are perforations made by the pins which hold the blocks together and are not included in the footings.

FIG. 1.—A reduced copy of a single record-sheet, containing first four trials of experiment 27.

The blue and white (or normal) atherinas were divided into lots of 10 (5 blue and 5 white), and these lots were thrown to the snappers in succession, a new lot as soon as all the fish of the preceding lot had been taken. The order in which the blue and white fish were taken was recorded by means of the device described above and in the form shown in fig. 1. Twenty-two trials were made. The records of the first 14 were discarded because it was observed that the white fish sank more readily than the blue, so that a position error was included. In the remaining 8 trials all the atherinas were made heavier than sea-water by laying open the air-bladder and emptying it by compression. All sank when thrown. These 8 trials appear in table 3, which shows the total number of blue and white atherinas

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Fig. 3.

Fig. 4.

Fig. 3. French grunts, *Hæmulon flavolineatum*, blue and yellow striped, among coral rocks at base of reef. At right a snapper (*Lutianus apodus?*) banded with black and yellow.

Fig. 4. An undetermined labroid feeding on rock bottom; at its left a branching gorgonian, *Plexaura*.

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taken in each order by a colony of 100 gray snappers, at the west lighthouse dock, July 21, 8^h to 8^h 30^m a. m., when thrown in lots of 10, 5 white and 5 blue; the last 8 of 22 trials; 80 atherinas thrown; all taken.

TABLE 3.

Color.	Order or place.												Grand total.
	I.	II.	III.	IV.	V.	Total first 5 orders.	VI.	VII.	VIII.	IX.	X.	Total second 5 orders.	
Blue.....	0	0	1	0	5	6	2	8	8	8	8	34	40
White.....	8	8	7	8	3	34	6	0	0	0	0	6	40
													80

The Roman numerals indicate the orders or places for the fish of each color. The Arabic numerals show the number of times that fish of each color were taken in each order; they are the footings for each color of the vertical columns of the original record for the 8 trials included in the table.

From table 3 it appears that in all of the 8 trials the first and second and fourth fish to be taken were white. In 7 trials the third fish taken was also white; in 1 trial blue was third. In every trial of the 8 the seventh, eighth, ninth, and tenth fish taken were blue. In the first 5 orders white fish were taken 34 times out of a possible 40, that is, 85 per cent of the fish taken in the first 5 orders were white, while but 6, or 15 per cent, were blue. In the second 5 orders these numbers were reversed; 85 per cent of the fish taken are here blue and 15 per cent white. Of the blue fish 32, or 80 per cent, remained untaken until the last white fish was taken.

The atherinas used in the experiment were of practically uniform size; they had like taste (sour); those of the two colors sank and were intermingled at random in each trial. The only constant difference between them was one of color. In taking 85 per cent of white fish in the first 5 orders, while blue fish are still present, and in leaving 80 per cent of the blue fish until all the white had been taken, the snappers show clearly that they discriminate between the blue and white fish. It does not follow that they discriminate between the colors blue and white. The blue fish are darker than the white; brightness may therefore be the basis of discrimination rather than color tone. This point can not be determined in experiments involving blue and white only. It is discussed in another place in this paper and reasons are given for regarding the blue-white discrimination as one of color.

Experiment 27: Blue and red color discrimination.—In this and the following experiments of 1907 the atherinas used had been preserved in formalin and subsequently soaked in fresh water to remove the formalin. It is believed that enough formalin remained to give to all the atherinas like qualities in respect to taste or odor.

The atherinas used were all females of nearly the same size and were made to float by the following procedure: The viscera were removed through

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a longitudinal incision made with scissors through the body wall on one side from in front of the shoulder girdle to behind the vent. The body wall, stiffened by formalin, sprang back into place and the air inclosed by it made the fish float. The incision was made in a plane extending latero-ventrally, so that its edges were as oblique as possible. The ventral edge was thus overlapped and held in place by the dorsal and acted as a valve to retain the air.

Table 4 gives the result of an experiment in which both dark and light red were offered with blue to a colony of about 100 snappers at the east lighthouse dock. The snappers were first fed slowly for about 15 minutes on blue atherinas, both to dull their appetite and to familiarize them with the blue color. About 80 blue atherinas were thus fed before the blue-light-red trials, which began at 10 a. m. The 5 trials of blue and light-red atherinas followed at once on the preliminary feeding. An interval averaging about 5 minutes was allowed to elapse between the trials and during each interval 15 or 20 blue atherinas were fed. In the blue-light-red part of the experiment the 100 snappers thus had offered them 80 blue fish in the preliminary feeding, $9 \times 15 = 135$ blues in the interval-feeding, and 25 blues included in the 5 trials, or a total of 240; while but 25 reds were offered. All the 265 fish offered were taken.

The six blue-dark-red trials were begun at $4^h\ 12^m$ p. m. of the same day, after a preliminary feeding of 30 blue fish. The last trial included but 4 fish of each color, so that the total number of blue fish offered in this blue-dark-red part of the experiment was 194 as against 29 reds.

The method of staining the atherinas was that employed in experiment 26. The reds were stained as in experiment 1. The light red was obtained by a shorter stay in the stain. In order to determine the relative brightness of the colors used the colored fish were matched with cardboard disks stained with the same dyes and these were compared on a color wheel with grays in the usual manner and with the following result: The blue was equivalent in brightness to a gray containing 65 per cent black; the light red to a gray containing 50 per cent black; the dark red to a gray containing 75 per cent black.

The experiment with the snappers was conducted in bright sunlight. A considerable portion of this light does not penetrate into the water, but is reflected from its surface. The snappers, moreover, view the colored fish from beneath. They see the side which is illuminated by light reflected upward from the white sand bottom. The intensity of this illumination was estimated by examining the floating colored atherinas from below by means of the reflecting water-glass described in the footnote on page 298. The brightness of the colors used was then measured in a light which was judged to be of the same intensity as that which illuminated the colored atherinas in the actual experiment.

Table 4 shows the total number of blue and red atherinas taken in each

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order by a colony of 100 gray snappers at the east lighthouse dock, July 24, 1907. The experiment includes a blue-light-red series of 5 trials and blue-dark-red series of 6 trials—each trial of 10 fish—5 blue, 5 red. The last blue-dark-red trial of 8 fish only. Blue-light-red trials began at 10 a. m.; blue-dark-red at 4^h 12^m p. m.

TABLE 4.

Color.	Order or place. I.	II.	III.	IV.	V.	Total first 5 orders.	VI.	VII.	VIII.	IX.	X.	Total second 5 orders.	Grand totals.
Blue.....	4	5	3	4	5	21	3	0	1	0	0	4	25 } 50
Light-red...	*1	0	2	1	0	4	2	5	4	5	5	21	25 }
Blue.....	6	6	6	5	3	26	3	0	0	0	0	3	29 } 58
Dark-red†..	0	0	0	1	3	4	3	6	6	5	5	25	29 }
													108

* This fish sank.
† All 5 reds of the first trial and 3 of the second were untaken; they are included in the table as though taken after the blues.

In this experiment errors due to possible differences in the chemical properties of the fish of the two colors seem to be eliminated by the preservation in formalin and by the use of acetic acid in staining; errors of size are eliminated by use of mature female atherinas of practically uniform size; errors of position are eliminated by the random mingling of the blue and red atherinas all floating at the surface. The snappers have clearly chosen the more familiar blue in preference to both a lighter and a darker red. Thus 21, or 84 per cent, of the blue fish are taken in the first 5 orders when offered with light red, and but 4, or 16 per cent, in the second 5 orders; 26, or about 90 per cent, of the blue fish are taken in the first 5 orders when offered with dark red, while but 3, or 10 per cent, are taken in the second 5 orders. I can interpret the result only as showing blue-red color-vision.

To an observer the behavior of the snappers is quite as convincing as the tabulated data. Repeatedly when a blue and a red fish floated near one another, but at some distance from other atherinas, a snapper after swimming about beneath them for considerable time, as though examining both, took the blue. If in any such case during this experiment the red fish was the first of the two to be taken the fact escaped me. Repeatedly, too, snappers approached red fish and then jerked back and did not take them, but a similar behavior toward the blue was not observed.

Experiment 28: Blue and green color discrimination.—By July 25, 1907, all 3 colonies of snappers had become so experienced in atherinas preserved in formalin that they took them slowly, and after taking a limited number in any one experiment, refused them altogether. The remaining experiments were thus necessarily each restricted to but few trials.

On the afternoon of July 25 blue, prepared as in experiment 26, was offered with both light and dark green, all made to float. The greens were

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obtained by the use of Diamond package dye, fast dark green, used in accordance with the directions on the package. The brightness of the 3 colors was found on the color-wheel to be as follows: the blue equivalent to a gray containing 79.5 per cent black; the light green to a gray containing 51 per cent black; the dark green to a gray containing 79 per cent black.

After the snappers had been fed on blue atherinas for about 10 minutes 2 trials were made with the blue and light green, followed by one with the blue and dark green. The results are given in table 5, which shows the total number of blue and green atherinas taken in each order by a colony of 100 gray snappers at the east lighthouse dock, July 24, 1907. The experiment included a blue-light-green series of two trials, and a single blue-dark-green trial, each trial of 10 fish—5 blue, 5 green.

TABLE 5.

Color.	Order or place.											Grand total.
	I.	II.	III.	IV.	V.	Total first 5 orders.	VI.	VII.	VIII.	IX.	X.	Total second 5 orders.	
Blue	1	1	0	0	2	5	1	0	1	2	1	5	10 } 20
Light green	0	1	2	2	0	5	1	2	1	0	1	5	10
Blue	1	0	0	1	1	3	1	0	1	0	0	2	5 } 10
Dark green	0	1	1	0	0	2	0	1	0	1	1	3	5
													30

Table 5 gives no evidence of a discrimination between the blue and green colors used. These colors were, however, impure, the green including some blue and the blue including some green. To my own eye they were widely different, but other members of the Tortugas staff found difficulty in distinguishing between the blue and dark-green fish as they floated over the snappers. It is quite possible that the snappers would discriminate between a spectral blue and a spectral green if it were possible to experiment with these colors by this method. The blue-green trials are, however, of interest as showing lack of discrimination on the basis of brightness, for here the blue and dark green are of the same brightness, while the light-green is much brighter, and yet there is no evidence of discrimination.

Immediately after the trial of blue and dark green recorded in table 5 a single trial was made of red and blue floating atherinas. These 10 fish were taken in the following order: R, B, B, B, B, B; 4 red fish remained untaken. The record, as well as the difference in the behavior of the snappers toward the two colors, shows clearly that they discriminate between them.

Experiment 29: Blue and yellow color discrimination.—On July 26 snappers in all three colonies took blue formalin atherinas so slowly at 7 a. m. that discrimination experiments could not be undertaken. At 11 a. m. the snappers at the Laboratory dock were found to take both floating and sinking blue fish with some interest. After feeding them on blue for about

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4 minutes, 3 trials were made in which a choice was offered of blue and yellow. The blue atherinas were prepared as in experiment 26 and were of a shade equivalent to a gray containing 65 per cent black. The yellow fish were stained in Diamond package dye, fast yellow, according to directions on the package. It was equivalent in brightness to a gray containing 53 per cent of black. The fish of both colors had been treated with acetic acid in the staining and were therefore of like taste. They were of the same size and all, except one yellow, floated. The result of the experiments is shown in table 6. I was unable with the materials at command to obtain a yellow darker than the blue. The snappers in all three colonies had, moreover, now become so familiar with the unpalatability of colored formalin fish that further experiments with them could not be made. When it is remembered that in the red-blue experiments the snappers discriminated between the atherinas on account of their color tone, not on account of their brightness, and that in the green-blue experiments they fail to discriminate on account of brightness, it seems to me that in spite of the small number of atherinas included, table 6 shows clearly a power of discrimination between the blue and yellow used. The experiment includes 3 trials of 10 fish each—5 blue, 5 yellow.

TABLE 6.—*Total number of blue and yellow atherinas taken in each order by a colony of 150 gray snappers at the Laboratory dock, July 26, 1907.*

Color.	Order or place.											Grand totals.
	I.	II.	III.	IV.	V.	Total first 5 orders.	VI.	VII.	VIII.	IX.	X.	Total second 5 orders.	
Blue.....	3	3	2	2	1	11	1	1	1	0	0	3	*14
Yellow.....	0	0	1	1	2	4	2	1	1	2	2	8	*12
													*26

* 1 blue and 3 yellow remained untaken in the last throw and are not included in the table, which therefore includes 26 fish instead of 30. 1 yellow remained untaken in the first throw and 4 in the second; these are included in the table as though taken after the blues of their respective trials.

Here again the behavior of the snappers was even more conclusive, as the following extract from my notes, referring to experiment 29, shows:

After feeding on blue for some time (3 or 4 minutes) they were offered blue and yellow in lots 10 (5 each). A distinct preference developed for the blue. The snappers showed little interest in the yellow, leaving fish of that color largely unnoticed, but swimming about under the blue until finally taken. One yellow sank and was examined perhaps 50 times by various snappers, but remained untaken on the bottom. The yellows were left for the most part apparently unnoticed, but when one was approached the fish jerked back from it. All besides myself who watched the experiment agree that the behavior of the fish shows more clearly than the actual record that they discriminate yellow and blue. This colony had had no previous experience with yellow atherinas.

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COLOR DISCRIMINATION EXPERIMENTS (1905).

I am unable to interpret the experiments of 1907, except as showing color-vision in the gray snapper. The experiments of 1905 are here added because, while following a somewhat different method, their results are in accord with those of the later experiments. These experiments differ from those of 1907 as follows:

(*a*) The atherinas used were fresh, as in experiment 26 of 1907.

(*b*) The preliminary feeding was therefore larger and usually included 300 or 400 atherinas.

(*c*) The series of trials was much longer, because the fresh fish were taken more readily.

(*d*) Some of the atherinas sank, while the others floated. If those of one color had sunk more frequently than those of the other color there would have been introduced an error of position. This was not known to happen except in the first 14 trials of experiment 26 above, which were therefore discarded. It is unlikely that in a long series of trials fish of one color sank more frequently than those of the other.

(*e*) The order in which the atherinas were taken was called out by the observer and recorded by an assistant. The observer called, for instance, white, white, white, blue, white, blue, blue, white, blue, blue (see under trial I, table 7). The recorder gave serial numbers to the colors as called and entered them opposite the name of the color in a previously prepared blank. A portion of such a record representing 5 successive trials of a single experiment is reproduced in table 7, which is part of an original record showing the order in which blue and white atherinas were taken in 5 successive trials in each of which 5 white and 5 blue fish were thrown.

TABLE 7.

	Trial I.	Trial II.	Trial III.	Trial IV.	Trial V.
Blue.....	4 6 7 9 10	3 6 8 9 10	1 7 8 9 10	2 3 6 9 10	2 3 5 7 10
White.....	1 2 3 5 8	1 2 4 5 7	2 3 4 5 6	1 4 5 7 8	1 4 6 8 9

The results of each experiment were then tabulated to show in how many trials fish of each color were taken first, second, third, etc. Table 8 shows the result of two series of trials made on the morning of July 20, 1905. The table shows the same discrimination between blue and white that appeared in table 3, but less marked. I have no doubt that this difference in results when using fresh and preserved atherinas gages accurately the discrimination of the snappers in the two cases. The greater palatability of the fresh atherinas results in those of the two colors being taken more indiscriminately, even though the color differences are perceived. With the less palatable formalin atherinas the snappers not only distinguish the colors, but discriminate more sharply between familiar and unfamiliar. There is this further difference between the experiments of 1905 with fresh atherinas and those of later date with formalin atherinas. Some of the fresh fish float; others sink, and are thus brought nearer the snappers and taken

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first. There is no reason to believe that those of one color sink more frequently than those of the other, so that the sinking introduces no constant error. It does increase the difficulty of making an accurate record, but here again errors doubtless occur as frequently with one color as with the other. The greater discrimination apparent in tables from experiments with formalin fish I believe, then, to be an expression of the reality, rather than of a difference in accuracy of method. Table 8 shows the total number of blue and white atherinas taken by 100 gray snappers in each order, when thrown in lots of 10—5 blue and 5 white—during 26 successive trials; 260 fish thrown; 5 remained untaken; July 20, 1905.

TABLE 8.

Color.	Order or place.												Grand totals.
	I.	II.	III.	IV.	V.	Total first 5 orders.	VI.	VII.	VIII.	IX.	X.	Total second 5 orders.	
Blue.....	7	7	15	16	11	56	9	11	19	12	20	71	127
White.....	19	19	11	10	15	74	17	15	6	11	5	54	128
													255

Experiment 30: Blue and white color discrimination.—This experiment was performed four times (July 19, 20, 21, 22), but the results were invariable, so that only the series of July 20 and 21 need be considered. In each series the trials were preceded by a feeding of fresh atherinas and were continued so long as the snappers took the food readily. The series followed one another from time to time during the day, as the appetite of the snappers permitted.

The results of the four series of July 20 are plotted in table 9. The data were first arranged in a table of the form of table 8, which combines the first two series of July 20. The number of times that blue and white fish were taken in each order was then calculated from the table in percentages of the maximum number of times that it might be taken in that order, that is, in percentages of the total number of trials involved in each series of trials of the experiment. The diagram (table 9) shows in percentages the frequency with which a colony of 100 gray snappers took blue or white atherinas in each order in 4 series of trials including 460 atherinas. The atherinas were thrown in lots of 10—5 white and 5 blue together. The percentage of fish of each color taken in each order is calculated for each series separately on the basis of the total number of times that fish of each color might have been taken in each order, *i. e.*, on the basis of the number of trials in each series. This basis is in series I, 7; in series II, 19; in series III, 5; in series IV, 15.

The solid line represents the white fish, the broken line the blue fish. The divisions on the ordinate at the left represent percentages; while in

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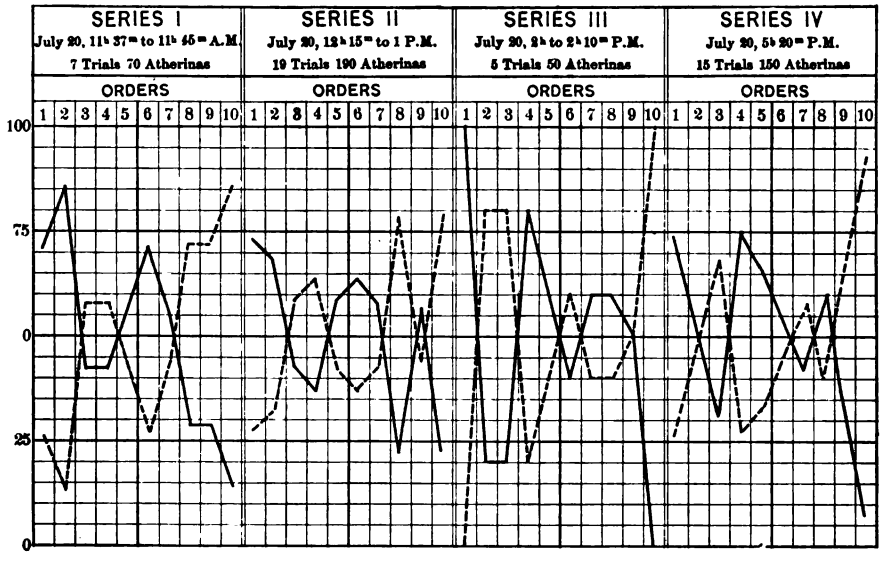
each series the columns numbered from 1 to 10 represent the orders. This table shows in percentages for each of the four series of trials made on this day what is shown in table 8 for series I and II combined. If the snappers had, in each trial, taken all the white fish before taking any of the blue, then the solid line would run along the 100 per cent level through the first 5 spaces of each series of trials, while the broken line would continue along the same level through the second 5 spaces. Probably if a single snapper could be experimented upon with so large a number of atherinas such a result would be reached. In an experiment involving 100 snappers they are crowded together, so that the effort of each to get first at the food stimulates the others. Apparently as a result of this competi-

TABLE 9.



tion a snapper frequently takes the nearest atherina, whatever its color, so that blue fish are often taken while white fish are still present. It results that the solid line starts usually somewhere near the 75 per cent level and zigzags downward toward the zero level, while the broken line starts usually near the 25 per cent level and zigzags upward toward the 100 per cent level.

If the snappers had taken the blue fish as frequently in each order as the white, that is, had not distinguished at all between them, the solid and broken lines would coincide with one another and both would run on the 50 per cent level through the entire 10 spaces of each series of trials. If the snappers tended in the successive series of the experiment to take white and blue fish more and more indiscriminately, then in the later series there should be evident an increasing tendency for the broken and solid lines to

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Fig. 5.

Fig. 6.

Fig. 5. Two blue surgeons, *Hepatus cæruleus*, and a *Chætodon ocellatus* in front of branching gorgonian, *Plexaura*.

Fig. 6. A *Chætodon capistratus* over incrusting coral, *Mæandrina*, and in front of large Gorgonian.

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coincide at the 50 per cent level. No such tendency appears in the diagram. Such a tendency of the two lines to approximate each other and the 50 per cent level more in the final series of the experiment than in the earlier series would then be evidence that the snappers rapidly learn the equal palatability of the blue and white atherinas. In only one respect do the lines seem to afford possible evidence that the snappers tend to discriminate less between the white and blue fish toward the end of the day's experiment. This is in the crossing of the solid and broken lines at a point which is nearer the ordinate of percentages in series III and IV than in series I and II. The two lines come together more rapidly in the third and fourth series than in the first and second. The series of July 19, 21, and 22 have also been plotted. The series of July 19 and 21 do not afford the evidence apparently shown in that of July 20 of a decrease of discrimination during a single day, nor does the series of July 22 when compared with those of earlier date show any decrease of discrimination from day to day. If the snappers could be isolated from the living atherinas which they have constantly in view, and if they could be fed continuously on blue and white fish in equal numbers, they might soon take the one in each place as frequently as the other, but with the living white fish constantly in sight as part of the natural environment, and with the blue supplied only at intervals and for a short time, this result is not to be expected.

Experiment 31: Blue and red color discrimination.—On July 21 two series of blue and white discrimination trials were made, the first at $8^h\ 7^m$ a. m., and the second at $2^h\ 40^m$ p. m. Three hundred and sixty atherians were used in addition to those involved in two preliminary feedings of normal fish. The results, as plotted in table 10, series I and II, do not differ from those shown in table 9. Immediately after the second series of 12 trials with blue and white fish there followed a series of 10 trials (involving 100 atherinas) in which red fish were substituted for the white, so that, whereas the snappers had before had a choice between white and blue and had become familiar with blue, they now had a choice between red and blue. The red atherinas were prepared as in experiment 2 and had therefore the same acid taste as the blue. The results are plotted as series III of the experiment of July 21 and are shown in table 10. The blue fish are represented as before by the broken line, while the red fish are represented by a line of dots and dashes. It is seen that the broken line occupies in series IV the position of the solid line in series I and II. The line of dots and dashes representing the red fish occupies, on the other hand, the position taken in series I and II by the broken line which represents the blue fish. In other words, the blue fish are now taken more frequently than the red in the first four orders. Blue is taken first in 70 per cent of the trials, while red is taken first in but 30 per cent. It is further to be noted that not only is the position of the broken line reversed in series III as compared with

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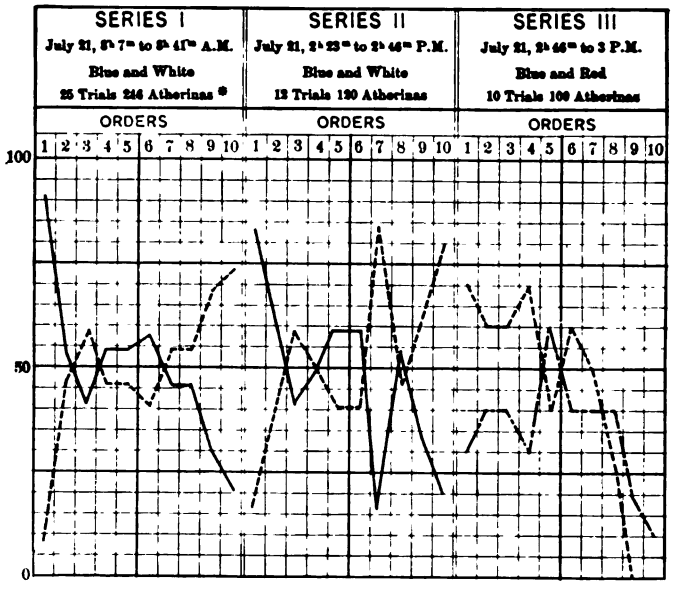
series I and II, but it first intersects the line of dots and dashes at a point farther from the ordinate of percentages than in series II and III, a further evidence of discrimination. Of the 100 fish thrown in the 10 trials of series III, 21 remained untaken or were eliminated from the experiment through an error of the record. Of the 79 fish taken, 44 were blue and 35 were red; 30 blue fish were taken in the first 5 places as against 20 red, while 14 blue fish were taken in the second 5 places as against 15 red; 16 fish remained untaken at the close of the experiment, and of these 12 were red, while 4 were blue fish to which a small amount of red stain had been accidentally transferred. The diagram (table 10) shows in percentages in each order the

TABLE 10.


SERIES I
July 21, 2h 7m to 2h 41m A.M.
Blue and White
25 Trials 246 Atherinas
SERIES II
July 21, 2h 23m to 2h 46m P.M.
Blue and White
13 Trials 120 Atherinas
SERIES III
July 21, 2h 46m to 3 P.M.
Blue and Red
10 Trials 100 Atherinas
ORDERS
ORDERS
ORDERS
1 2 3 4 5 6 7 8 9 10 1 2 3 4 5 6 7 8 9 10 1 2 3 4 5 6 7 8 9 10
100
50
0

frequency with which a colony of 100 gray snappers took atherinas in each order in three series of trials. The atherinas were thrown in lots of 10. In the first two series 5 white and 5 blue were thrown together; in the third series 5 blue and 5 red were thrown together. Percentages are calculated as in table 9; 21 atherinas remained untaken in the third trial.

The plotted data seem to show conclusively that the fish discriminate between the red and blue atherinas. The approximation of the two lines in the second half of their course in series III and their descent toward the zero level is due to the fact that the snappers were at this time no longer hungry, took any but normal fish very slowly, and left many untaken. The behavior of the snappers toward the red and blue fish is further proof of discrimination, as shown by the following extract from my notes:

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The difference in the behavior of the fish toward red and blue was very noticeable. They were from the first distinctly afraid of the red and took them only when they sank so that they could put the snout directly against them as though smelling. Even then they often jerked back, as does a horse under like circumstances, and did not take the fish at all, but left it to be taken by another, or perhaps took it after one or two attempts. The blue fish were all taken at once, and without preliminary "smelling." They were taken quickly. The red were taken slowly, the snappers often running a little distance with them as though gingerly tasting and then finally swallowing them.

Such hesitation as the snappers showed in taking the red fish in this experiment is to be expected even toward normal fish at the close of any experiment involving liberal feeding. The evidence of discrimination lies in the very much greater hesitation shown toward the red fish than toward the blue at the beginning of series III. The hesitation itself is merely the normal behavior of a satiated fish toward any new object in the environment, but the degree of hesitation is significant.

Since it is possible that the snappers discriminated between the red, white, and blue atherinas by reason of a difference in their luminosity or brightness and without distinguishing the colors themselves, it became necessary to determine the relative brightness of the colors employed. The following tests were made:

(1) The red, white, and blue fish were looked at against a black background in a light so feeble that colors could not be distinguished. Their brightness diminished in the order white, red, blue.

(2) Disks of cardboard were colored with the red and blue stains to match the red and blue fish and the brightness of each of these disks was then determined by the same person by comparing it on a color-wheel to a gray produced by blending black and white in known proportions. Ninety-seven degrees of white to 263 degrees of black matched the red in brightness, while 37 degrees of white and 323 degrees of black matched the blue. The luminosity of the blue compared to that of the red is therefore expressed by the fraction

$$\frac{37 \times 60 + 323}{97 \times 60 + 263} = \frac{2543 \text{ blue}}{6083 \text{ red}} \quad \text{or approximately 5 to 12.}$$

(3) A spectroscopic examination[1] was made by transmitted light of the dyes used and also by reflected light of pieces of cardboard stained to match the atherinas. For the latter purpose the apparatus of Mayer (1897) was used. The red was found to include light of wave-lengths between 675$\mu\mu$ to 595$\mu\mu$, while the blue included in moderate illumination light of wave-lengths between 590$\mu\mu$ and 451$\mu\mu$. A comparison of these wave-lengths with Koenig's diagram as given by Howell (1906) shows that the red falls in the most luminous part of the spectrum, while the blue falls in the least luminous part.

[1] I am indebted to Dean John O. Reed, Professor of Physics in the University of Michigan, for calibrating the spectroscope used.

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Since in the color-discrimination experiments 30 and 31, the snappers preferred the white to the blue and the blue to the red, they choose in the first case the brighter fish and in the second case those less bright. They were therefore guided not by the brightness of the fish, but by their color. Had time permitted and material been available the experiments of 1905 with fresh atherinas would have been extended so as to include a red-blue series in which the red was the darker color. Other colors would also have been used.

DISCUSSION OF COLOR DISCRIMINATION EXPERIMENTS.

The colors used in the experiments described were obtained by the use of dyes. They are impure, and I know of no dyes by which pure spectral colors may be obtained. The red used shows with the spectroscope rays of all wave-lengths below the green, while the blue shows waves of all lengths above the yellow. The yellow used is nearly pure, the green includes both yellow and blue rays. We may therefore conclude that the snappers discriminate between a mixture of colors of that part of the spectrum which lies below the green and a mixture of the colors of that part which lies above the yellow, and that they discriminate yellow from a mixture of the colors of the part of the spectrum above the yellow. Whether the particular mixtures used appear to the snapper as they do to us, we can not know from the experiments. On the other hand, these mixtures may appear to the snapper precisely as they do to us and his power of color discrimination may be as accurate for all colors as our own. The only paper known to me on color discrimination in fishes is that of Washburn and Bentley (1906), where results were obtained on a single individual of *Semotilus atromaculatus*. The fish was kept in an aquarium and the methods were those of the laboratory. The results are in accord with my own. The literature of the subject is discussed by Washburn and Bentley.

VI. ESTABLISHMENT IN THE GRAY SNAPPER OF A WARNING COLOR REACTION, INVOLVING AN ASSOCIATION BETWEEN COLOR AND UNPALATABILITY.

In the experiments described in this section red atherinas were rendered unpalatable and were then fed to the Laboratory colony of gray snappers, in order to learn whether the snappers would form an association between the unpalatability of the atherinas and their color, of such a sort that they would refuse the atherinas at sight, *i. e.*, by reason of their color alone. If this should prove to be the case the color red would have come to have for the gray snapper a warning significance experimentally established under normal conditions.

In some of the preliminary experiments the red atherinas were rendered unpalatable by the use of substances not normal to the environment of the

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snapper, such as quinine and red pepper. So far as the experiments went the snappers gave no evidence that these substances were distasteful. A few attempts to feed to the snappers the tissues of the medusa *Cassiopea xamachana* showed them to be distinctly unpalatable. However disguised in form or color they were rejected after a few trials, presumably on account of the contained nettle-cells. The red atherinas were then made unpalatable by sewing into the mouth of each the branching tip of a tentacle of this medusa. The tentacle had the appearance of food projecting slightly from the mouth. The atherinas thus prepared were thrown from the dock, one at a time, to the assembled colony of about 150 snappers. An additional atherina was thrown as soon as its predecessor had been taken or as soon as the behavior of the snappers showed that it would not be immediately taken. The snappers thus had at least one atherina always before them. A record was kept of the behavior of the snappers toward each atherina offered.

Experiment 32.—Occupied 3 days, July 16, 18, and 19, 1907, but is best regarded as a single experiment. The atherinas used had been preserved in 2 per cent formalin. They were rinsed and then allowed to soak for about 2 hours in a large quantity of sea-water. A few of these when offered to the snappers were taken as though fresh. Tentacles of *Cassiopea* were sewn into the mouths of others in such a way as to leave the fringed end of the tentacle projecting. The tentacled fish were then stained in fast scarlet in the manner described for experiment 1, until they were of a brilliant red color. The effect of this treatment upon the nettle-cells was not positively determined, but the result of the experiment indicates that they remained active.

Atherinas prepared in this way are referred to as *formalin tentacled reds;* fish similarly prepared but without tentacles are referred to as *formalin reds;* those prepared in formalin and washed but not stained are referred to as *formalin normals;* while formalin fish provided with tentacle but unstained are referred to as *formalin tentacled normals.* The behavior of the snappers toward each atherina offered them was recorded under one of the four heads (table 11); *taken at once* indicates that the atherina was seized as soon as it struck the water; *taken with hesitation,* that 1 to 3 seconds passed before the atherina was seized; *taken with much hesitation,* that more than about 3 seconds passed before the atherina was seized; *refused* indicates that the atherina remained untaken during the time of the series to which it belonged, or else that after the snappers had had abundant opportunity to take it, the tide carried it away, so that it could no longer be observed. Several minutes were required for an atherina to be thus carried away, and this happened only during the first two series of the experiment, in which some of the atherinas floated while others sank. In the third series the atherinas were made to sink by slitting the air bladder so that all that remained untaken were accessible to the snappers during the series and for some time afterward.

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TABLE II.

Series I, July 16, 1907, 11h30m a. m. to 12h05m p. m.; 35 minutes.

Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused.	Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused.	Serial Nos.	At once	Hesitation.	Much hesitation.	Refused.
1	N	...	...	...	61	...	...	T	...	121	N	...	...	...
	N	...	...	...		...	T	...	...		N	...	...	...
	N	...	...	...		...	...	T	...		N	...	...	...
	T	...	...	...		...	T	...	...			...	...	...
	T	...	...	...		...	...	T	...			...	...	...
	...	...	...	T		...	T	...	...			...	...	...
	...	...	T	...		...	T	...	..			...	...	...
	T	...	...	...		...	...	T	...			...	...	...
	T	...	...	...		...	...	T	...			...	...	...
10	T	...	...	...	70	...	...	T	...	130	...	...	...	...
	T	...	...	...		...	...	T	...			...	...	...
	...	...	T	...		...	...	...	T			...	...	...
	...	...	T	...		...	...	T	...			...	...	...
	T	...	...	...		...	...	T	...			...	...	...
	T	...	...	...		...	...	...	T			...	...	...
	T	...	...	...		...	T	...	...			...	...	...
	...	...	...	T		...	T	...	...			...	...	...
	...	...	T	...		...	T	...	...			...	...	...
	...	...	T	...		...	T	...	...			...	...	...
20	...	...	T	...	80	...	...	...	T	140	...	...	...	...
	...	...	T	...		...	...	...	T			...	...	...
	...	...	T	...		...	...	...	T			...	...	...
	...	T	...	...		...	...	T	...			...	...	...
	...	...	T	...		...	...	R	...			...	...	...
	...	...	T	...		...	...	R	...			...	...	...
	...	...	T	...		...	...	R	...			...	...	...
	...	T	...	...		...	...	R	...			...	...	...
	...	T	...	...		...	...	R	...			...	...	...
	...	T	...	...		...	...	R	...			...	...	...
	...	T	...	...		...	...	R	...			...	...	...
30	...	T	...	...	90	...	...	R	...	150	...	...	...	...
	...	T	...	...		...	...	...	R		...	...	...	...
	...	T	...	...		...	...	R	...		...	...	...	...
	...	T	...	...		...	...	...	R		...	...	...	...
	...	T	...	...		...	...	R	...		...	...	...	...
	...	...	T	...		...	...	...	R		...	...	...	...
	...	...	...	T		...	...	...	R		...	...	...	...
	...	...	...	T		...	...	R	...		...	...	...	...
	...	T	...	...		...	...	R	...		...	...	...	...
	...	T	...	...		...	...	R	...		...	...	...	...
40	...	T	...	...	100	...	...	R	...	160	...	...	...	...
	...	...	T	...		...	...	...	R		...	...	...	...
	...	...	...	T		...	...	...	R		...	...	...	...
	...	T	...	...		...	...	...	R		...	...	...	...
	...	T	...	...		N	...	...	...		...	...	...	...
	...	T	...	...		N	...	...	...		...	...	...	...
	...	...	T	...		N	...	...	...		...	...	...	...
	...	...	...	T		N	...	...	...		...	...	...	...
	...	...	T	...		N	...	...	...		...	...	...	...
	...	...	...	T		N	...	...	...		...	...	...	...
50	...	...	...	T	110	N	...	...	...	170	...	...	...	...
	...	...	...	T		N	...	...	...		...	...	...	...
	...	T	...	...		N	...	...	...		...	...	...	...
	T	...	...	...		N	...	...	...		...	...	...	...
	...	T	...	...		N	...	...	...		...	...	...	...
	...	T	...	...		N	...	...	...		...	...	...	...
	...	...	T	...		N	...	...	...		...	...	...	...
	...	T	...	...		N	...	...	...		...	...	...	...
	...	...	T	...		N	...	...	...		...	..	...	...
	...	T	...	...		N	...	...	...		...	...	...	...
60	...	...	...	T	120	N	...	...	...	180	...	...	...	...

Digitized by Google

TABLE II—Continued.

Series II, July 18, 1907, 12h30m to 12h40m p. m.; 10 minutes.

Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused.	Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused	Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused.
1	N	...	...	...	61	...	R	...	...	121	N	...	...	...
	N	...	...	...		R	...	...	...		N	...	...	...
	N	...	...	...		R	...	...	...		N	...	...	...
	N	...	...	...		...	R	...	...		N	...	...	...
	N	...	...	...		R	...	...	...		N	...	...	...
	N	...	...	...		...	R	...	...		N	...	...	...
	N	...	...	...		...	...	R	...		...	...	...	...
	N	...	...	...		...	...	R	...		...	...	...	...
	N	...	...	...		...	R	...	...		...	...	...	...
10	N	...	...	...	70	...	R	...	...	130	...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	...	R	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
20	R	...	...	...	80	...	R	...	...	140	...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	...
30	R	...	...	...	90	R	...	...	...	150	...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	..
	R	...	...	...		R	...	...	...		...	...	...	...
	...	R	...	...		R	...	...	...		...	...	...	...
40	...	R	...	...	100	R	...	...	...	160	...	...	...	...
	...	R	...	...		R	...	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
50	R	...	...	...	110	R	...	...	...	170	...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	...	...	R	...		...	R	...	...		...	...	..	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	...
	...	...	R	...		N	...	...	...		...	...	...	...
	...	...	R	...		N	...	...	...		...	...	...	...
	...	R	...	...		N	...	...	...		...	...	...	...
60	...	R	...	...	120	N	...	...	...	180	...	...	...	...

Digitized by Google

TABLE II.

Series I, July 16, 1907, 11h30m a. m. to 12h05m p. m.; 35 minutes.

Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused.	Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused.	Serial Nos.	At once	Hesitation.	Much hesitation.	Refused.
1	N	...	...	...	61	...	...	T	...	121	N	...	...	...
	N	...	...	...		...	T	...	...		N	...	...	...
	N	...	...	...		...	...	T	...		N	...	...	...
	T	...	...	...		...	T	...	...		...	...	...	...
	T	...	...	...		...	...	T	...		...	...	...	...
	...	...	...	T		...	T	...	...		...	...	...	...
	...	...	T	...		...	T	...	..		...	...	...	...
	T	...	...	...		...	...	T	...		...	...	...	...
	T	...	...	...		...	...	T	...		...	...	...	...
10	T	...	...	...	70	...	...	T	...	130	...	...	...	...
	T	...	...	...		...	...	T	...		...	...	...	...
	...	...	T	...		...	...	...	T		...	...	...	...
	...	...	T	...		...	...	T	...		...	...	...	...
	T	...	...	...		...	...	T	...		...	...	...	...
	T	...	...	...		...	...	...	T		...	...	...	...
	T	...	...	...		...	T	...	...		...	...	...	...
	...	...	...	T		...	T	...	...		...	...	...	...
	...	...	T	...		...	T	...	...		...	...	...	...
	...	...	T	...		...	T	...	...		...	...	...	...
20	...	...	T	...	80	...	...	...	T	140	...	...	...	...
	...	...	T	...		...	...	...	T		...	...	...	...
	...	...	T	...		...	...	...	T		...	...	...	...
	...	T	...	...		...	...	T	...		...	...	...	...
	...	...	T	...		...	...	R	...		...	...	...	...
	...	...	T	...		...	...	R	...		...	...	...	...
	...	...	T	...		...	...	R	...		...	...	...	...
	...	T	...	...		...	...	R	...		...	...	...	...
	...	T	...	...		...	...	R	...		...	...	...	...
	...	T	...	...		...	...	R	...		...	...	...	...
30	...	T	...	...	90	...	...	R	...	150	...	...	...	...
	...	T	...	...		...	...	...	R		...	...	...	...
	...	T	...	...		...	...	R	...		...	...	...	...
	...	T	...	...		...	...	...	R		...	...	...	...
	...	T	...	...		...	...	R	...		...	...	...	...
	...	...	T	...		...	...	...	R		...	...	...	...
	...	...	...	T		...	...	...	R		...	...	...	...
	...	...	...	T		...	...	R	...		...	...	...	...
	...	T	...	...		...	...	R	...		...	...	...	...
	...	T	...	...		...	...	R	...		...	...	...	...
40	...	T	...	...	100	...	...	R	...	160	...	...	...	...
	...	...	T	...		...	...	...	R		...	...	...	...
	...	...	...	T		...	...	...	R		...	...	...	...
	...	T	...	...		...	...	...	R		...	...	...	...
	...	T	...	...		N	...	...	...		...	...	...	...
	...	T	...	...		N	...	...	...		...	...	...	...
	...	...	T	...		N	...	...	...		...	...	...	...
	...	...	...	T		N	...	...	...		...	...	...	...
	...	...	T	...		N	...	...	...		...	...	...	...
	...	...	...	T		N	...	...	...		...	...	...	...
50	...	...	...	T	110	N	...	...	...	170	...	...	...	...
	...	...	...	T		N	...	...	...		...	...	...	...
	...	T	...	...		N	...	...	...		...	...	...	...
	T	...	...	...		N	...	...	...		...	...	...	...
	...	T	...	...		N	...	...	...		...	...	...	...
	...	T	...	...		N	...	...	...		...	...	...	...
	...	...	T	...		N	...	...	...		...	...	...	...
	...	T	...	...		N	...	...	...		...	...	...	...
	...	...	T	...		N	...	...	...		...	..	...	...
60	...	T	...	...		N	...	...	...		...	...	...	...
	...	...	...	T	120	N	...	...	...	180	...	...	...	...

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TABLE II—Continued.

Series II, July 18, 1907, 12h30m to 12h40m p. m.; 10 minutes.

Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused.	Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused.	Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused.
1	N	...	...	...	61	...	R	...	...	121	N	...	...	...
	N	...	...	...		R	...	...	...		N	...	...	...
	N	...	...	...		R	...	...	...		N	...	...	...
	N	...	...	...		...	R	...	...		N	...	...	...
	N	...	...	...		R	...	...	...		N	...	...	...
	N	...	...	...		...	R	...	...		N	...	...	...
	N	...	...	...		...	...	R	...		...	...	...	...
	N	...	...	...		...	...	R	...		...	...	...	...
	N	...	...	...		...	R	...	...		...	...	...	...
10	N	...	...	...	70	...	R	...	...	130	...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	...	R	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
20	R	...	...	...	80	...	R	...	...	140	...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	...
30	R	...	...	...	90	R	...	...	...	150	...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	..
	R	...	...	...		R	...	...	...		...	...	...	...
	...	R	...	...		R	...	...	...		...	...	...	...
40	...	R	...	...	100	R	...	...	...	160	...	...	...	...
	...	R	...	...		R	...	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
50	R	...	...	...	110	R	...	...	...	170	...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	...	...	R	...		...	R	...	...		...	...	..	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		...	R	...	...		...	...	...	...
	R	...	...	...		R	...	...	...		...	...	...	...
	...	...	R	...		N	...	...	...		.	...	...	...
	...	...	R	...		N	...	...	...		...	...	...	...
60	...	R	...	...	120	N	...	...	...	180	...	...	...	...

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TABLE II—Continued.

Series III, July 19, 1907, 10h40m to 11h30m a. m.; 50 minutes.

Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused.	Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused.	Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused.
1	N	...	...	...	61	...	T	...	...	121	...	...	T	...
	N	...	...	...		...	T	...	...		...	...	T	...
	N	...	...	...		...	...	T	...		...	T	...	...
	R	...	...	...		...	...	T	...		...	...	T	...
	R	...	...	...		...	...	T	...		...	...	...	T
	R	...	...	...		...	...	T	...		...	...	T	...
	R	...	...	...		...	T	...	...		...	...	...	T
	R	...	...	...		...	...	T	...		...	...	T	...
	R	...	...	...		...	T	...	...		...	...	T	...
10	R	...	...	...	70	...	...	T	...	130	...	...	T	...
	R	...	...	...		...	T	...	...		...	...	T	...
	R	...	...	...		...	...	T	...		...	...	T	...
	R	...	...	...		...	...	T	...		...	...	T	...
	T	...	...	...		...	...	...	T		...	...	T	...
	T	...	...	...		...	..	...	T		...	...	T	...
	T	...	...	...		...	...	...	T		...	...	T	...
	...	T	...	...		...	...	T	...		...	...	...	T
	...	T	...	...		...	...	T	...		...	...	T	...
	T	...	...	...		...	...	T	...		...	...	...	T
20	T	...	...	...	80	...	...	T	...	140	...	..	T	...
	...	T	...	...		...	...	T	...		...	...	T	...
	T	...	...	...		...	T	...	...		...	...	T	...
	...	T	...	...		...	...	...	T		...	...	...	T
	...	T	...	...		...	T	...	...		...	...	T	...
	...	...	...	T		...	T	...	...		...	...	T	...
	T	...	...	...		...	...	T	...		...	...	T	...
	...	...	T	...		...	T	...	...		...	T	...	...
	T	...	...	...		...	T	...	...		...	...	...	T
	...	...	...	T		...	T	...	...		...	...	...	T
30	...	T	...	...	90	...	T	...	...	150	...	...	T	...
	...	...	T	...		...	T	...	...		...	...	...	T
	...	...	T	...		...	...	...	T		...	...	T	...
	...	...	...	T		...	...	T	...		...	...	...	T
	...	T	...	...		...	...	...	T		...	...	T	...
	...	...	...	T		...	T	...	...		...	...	T	...
	...	...	T	...		...	T	...	...		...	...	...	T
	...	...	...	T		...	...	...	T		...	...	...	T
	...	...	T	...		...	T	...	...		...	...	...	T
	...	...	..	T		...	T	...	...		...	...	...	T
40	...	T	...	...	100	...	T	...	...	160	...	...	...	T
	...	...	...	T		...	...	T	...		...	...	...	T
	...	...	T	...		...	...	...	T		...	...	...	T
	...	T	..	...		...	T	...	...		...	...	...	T
	..	...	T	...		...	...	T	. .		...	...	...	T
	...	...	...	T		...	...	T	...		...	...	...	T
	...	T	...	...		...	...	T	...		...	...	...	T
	...	T	...	...		...	T	...	...		...	...	...	T
	...	T	...	...		...	...	T	...		...	...	...	T
	...	...	...	T		...	T	...	...		...	...	...	T
50	...	...	T	...	110	...	T	...	...	170	...	...	...	T
	...	...	...	T		...	T	...	...		...	...	...	T
	...	...	...	T		...	...	T	...		...	...	...	R
	...	...	T	...		...	...	T	...		...	...	...	R
	...	...	...	T		...	...	...	T		...	...	...	R
	...	...	T	...		...	T	...	...		...	...	...	R
	...	...	T	...		...	...	T	...		...	...	...	R
	...	...	T	...		...	T	...	...		...	...	...	R
	...	...	T	...		...	T	...	...		...	...	...	R
	...	T	...	...		...	...	T	...		N	...	...	...
60	..	...	T	...	120	...	T	...	...	180	N	...	...	...

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Fig. 7

Fig. 8

Fig. 9

Fig. 7. Two *Iridio bivittatus*, slippery dick, apparently black and white striped. French grunt beneath one in background.

Fig. 8. *Elacatinus oceanops*, in lower right hand corner clinging to massive coral, *Orbicella*, on outer face of reef. Expanded *Spirobranchus tricornis* at left.

Fig. 9. Gray snapper, *Lutianus Griseus*, over coral sand near shore.

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Digitized by Google

TABLE II, Series III—Continued.

Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused.	Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused.	Serial Nos.	At once.	Hesitation.	Much hesitation.	Refused.
181	N	...	...	...	201	N	...	...	...	221	...	...	..	...
	N	...	...	...		N	...	...	...		...	...	...	...
	N	...	...	...		N	...	...	...		...	...	...	...
	N	...	...	...		N	...	...	...		...	...	...	...
	N	...	...	...		N	...	...	...		...	...	...	...
	N	...	...	...		N	...	...	...		...	...	...	...
	N	...	...	...		N	...	...	...		...	...	...	...
	N	...	...	...		N	...	...	...		...	...	...	...
	N	...	...	...		...	...	...	...		...	...	...	...
190	N	...	...	...	210	...	...	...	...	230	...	...	...	...
	N	...	...	...		...	...	...	...		...	...	...	...
	N	...	...	...		...	...	...	...		...	...	...	...
	N	...	...	...		...	...	...	...		...	...	...	...
	N	...	...	...		...	...	...	...		...	...	...	...
	N	...	...	...		...	...	...	...		...	...	...	...
	N	...	...	...		...	...	...	...		...	...	...	...
	N	...	...	...		...	...	...	...		...	...	...	...
	N	...	...	...		...	...	...	...		...	...	...	...
	N	...	...	...		...	...	...	...		...	...	...	...
200	N	...	...	...	220	...	...	...	...	240	...	...	...	...

Table II shows behavior of the Laboratory colony of gray snappers toward each individual of 3 series of atherinas. N = formalin normal; R = formalin red; T = formalin tentacled red.

At the beginning of each series formalin normals were thrown to see whether the snappers were feeding with their usual avidity. These were followed, except in series II, by formalin tentacled reds and these in turn by formalin reds. The last atherinas thrown in each series were formalin normals.

Table II records the behavior of the snappers toward each individual of three series of atherinas. Here the normal fish are represented by the letter N, the formalin red by R, and the formalin tentacled red by T. Opposite the serial number of each atherina thrown it is represented by its appropriate letter placed in one of four columns; in the first if taken at once, the second if taken with hesitation, the third with much hesitation, fourth refused. The record of series I starts with 3 formalin normals all taken at once. These are followed by formalin tentacled reds. Of the first 13 of these, 9 are taken at once, 3 with much hesitation, and 1 refused. As the record continues it is seen that but 1 of these tentacled fish is afterwards taken at once, while the number taken with much hesitation and the number refused both increase toward the end. Of the 15 tentacled fish that were untaken, 11 are in the second 40 of the 80 tentacled fish thrown. The time required by the snappers to take tentacled fish thus increases as the series lengthens, so that the letters representing these fish shift more and more to the right in the 4 vertical columns. The untentacled red fish (R) follow the tentacled and it is seen that they are all refused or taken with

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much hesitation. They are treated like tentacled reds. They are followed in turn by formalin normals and these are all taken at once precisely as at the beginning of the series.

In series II formalin normals offered at the beginning are all taken at once. These are followed by formalin reds, a large number of which are taken at once, more especially in the first half of the series. Nearly all those taken with hesitation are in the second half of the series. Few are taken with great hesitation, and none are refused. Formalin normals offered at the end of the series are all taken at once. No tentacled fish were offered in this series and it has little bearing on the general result.

In series III formalin normals and formalin reds were both taken at once at the beginning. These were followed by formalin tentacled reds, only 8 of which were taken at once and these all in the first 15. Those after the first 15 were taken with hesitation, which increased as the series lengthened. All but 2 of the last 50 were either taken with great hesitation or refused. The last 16 were refused. Formalin reds offered immediately after the tentacled reds were all refused, while formalin normals following these were all taken at once. The behavior of the snappers toward red and white fish, which differ from each other only in color, is thus in striking contrast at the beginning and at the end of series III. At the beginning of the series the formalin reds are taken as readily as the formalin normals (white), but at the end, after the snappers have had experience of tentacled reds, formalin reds (untentacled) are refused, while formalin normals (white) are still taken. The fact that formalin normals are taken at once at the end of the series shows that any hesitation shown toward formalin tentacled reds earlier in the series is not due to loss of appetite. The snappers were hungry throughout each series. My notes record that formalin normals were taken at the end of series I, "and with the greatest avidity."

If either the first or third series could have been carried through on a single snapper, then presumably all the tentacled red fish taken would have fallen at the beginning of the series, the hesitation would then have gradually increased, and all the tentacled fish refused would have fallen at the end of the series. In an experiment dealing with a large number of snappers tentacled fish may be taken in any part of the series by snappers that have not yet had experience of them. Nevertheless, as shown in table 11, tentacled fish taken at once fall in the first part of each series. Thus in series I, all but one of the tentacled atherinas recorded as "taken at once" are in the first fourth of the tentacled part of the series. In series III, all the tentacled fish recorded as "taken at once" fall in the first tenth of the tentacled fish. On the other hand, tentacled fish "refused" fall chiefly near the end of each series. Thus in series I eleven fifteenths of those refused fall in the second half of the part of the series which they compose, while in series III about one-third of those refused fall at the end—a most significant fact.

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The three series shown in detail in table 11 are summarized in table 12, to show the total number of atherinas of each sort offered and the total number falling in each category. Series I requires no further comment. Series II has little bearing on the general result. It was introduced to determine whether the experience of the snappers with tentacled reds in series I had been of such a character as to lead them to refuse red atherinas even when not tentacled. This did not yet prove to be the case and all the red fish offered were taken, though less readily than the uncolored formalin normals.

TABLE 12.

Series and time.	Atherinas offered.	No. offered.	Taken at once.	Taken with hesitation.	Taken with much hesitation.	Refused.
Series I, July 16, 1907, 11h 30m a. m. to 12h 05m p. m.; *35 minutes.*	Formalin normals.....	3	3	0	0	0
	Formalin tentacled reds.	80	10	28	27	*15
	Formalin reds.....	20	0	0	13	* 7
	Formalin normals.....	20	20	0	0	0
	Total.....	123	.....	.....	.....	.....
Series II, July 18, 1907, 12h 30m to 12h 40m p. m.; *10 minutes.*	Formalin normals.....	10	10	0	0	0
	Formalin reds	106	59	41	6	0
	Formalin normals.....	10	10	0	0	0
	Total.....	126	.....	.....	.....	.....
Series III, July 19, 1907, 10h 40m to 11h 30m a. m.; *50 minutes.*	Formalin normals.....	3	3	0	0	0
	Formalin reds.....	10	10	0	0	0
	Formalin tentacled reds.	158	†8	20	85	§‡45
	Formalin reds	7	0	0	0	§ 7
	Formalin normals..	30	30	0	0	0
	Total.....	208	.....	.....	.....	.....

* The fish that remained untaken floated; although none of the formalin normals that floated remained untaken.
† Nos. 1, 2, 3, 6, 7, 9, 13, 15. ‡ Including Nos. 143 to 158. § All these fish sank.

All the atherinas used in series III were made to sink, so that tentacled fish that had been refused sank slowly through the colony of snappers and lay afterward on the bottom untouched. Seven formalin reds (without tentacles) were then offered and all were refused and remained untouched on the bottom. Immediately afterward 30 formalin normals were thrown. My notes record "all were taken as fast as fed, the first few with slight hesitation, the others immediately." The hesitation referred to was so slight that it does not appear in table 11.

An association between red and unpalatability thus appears to have been established in the individuals of this colony of 150 snappers. If we exclude series II this has resulted from 178 experiences of swallowing the tentacled fish. This is an average of but little more than one experience to each snapper. Series II closed at 11h 30m a. m. At 12h 15m p. m. a few formalin normals were thrown. The first were taken with a little hesitation, the others with a rush and without hesitation. Three formalin tentacled reds were then thrown; the first was taken with some hesitation, while

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the second and third were refused. Three formalin reds were then thrown and all refused. The 3 sorts of atherinas, 3 of each, were again offered immediately and in the same order. The formalin normals were taken, the reds, both tentacled and untentacled, were refused.

Since the tentacles project slightly from their mouths, formalin tentacled red atherinas differ from normal fish not only in color, but also in form. The snappers might therefore recognize them as unpalatable either by reason of their color or form or by both characteristics. That the snappers actually form an association between the disagreeable quality of the red tentacled atherinas and their color is shown by their refusal to take red atherinas which are not tentacled. As a further test, 20 formalin tentacled atherinas (uncolored) were offered to the laboratory colony of snappers at 1^h 15^m p. m. on July 19, 1907. Five formalin normals were first thrown and these were followed by the 20 formalin tentacled normals. All were taken without hesitation. Several red fish, some tentacled, others untentacled, were then thrown and remained for some time untaken, but were finally taken. The fact that white fish with tentacles are taken at once is evidence that the discrimination is by color, not by form. That red fish are still taken, though after much hesitation, is probably due in part to their having been offered immediately after a considerable number of formalin normals, in part to the presence in the colony of snappers whose individual experience of the unpalatable red was not yet sufficient to give to the color a warning significance. Such irregularities are to be expected in dealing in mass experiments with an entire colony of snappers. That experiment 32 gave to the color red a warning significance for the snappers, so that red atherinas were afterward for some time protected from their attacks by reason of their color, is shown in the next section of this paper.

The details of the behavior of the snappers toward the various sorts of atherinas used is of interest as enforcing the conclusion drawn from the tables and is here abstracted from my notes.

(*a*) *Formalin normals at the beginning of the series.*—The atherinas are taken when they strike the water. All the snappers rush at them and the successful fish snap so vigorously that they send spurts of water above the surface as they strike it with their tails in turning.

(*b*) *Formalin tentacled reds.*—These were taken quickly at first, but in a different manner from the formalin normals. The snappers did not rush at them with so much vigor as to produce a splash at the surface. As the feeding continued the tentacled reds were taken with increasing hesitation. Most of those taken were then approached deliberately. If the approach brought the snapper into contact with the tentacles he at once jerked back. This he sometimes appeared to do without contact with the tentacles. Sometimes the snapper jerked back upon contact with the sides of the atherina. This approach and retreat was often several times repeated by the same snapper. If an atherina was taken after being thus approached it was taken gingerly by the side or tail in such a way that the snapper did not come into

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contact with the tentacles. It was carried a little way, protruding from the mouth, and then slowly swallowed. After approaching an atherina and jerking back from it one or more times it often happened that a snapper swam away. The atherina might then be approached by many snappers in turn before being finally taken. The time taken by one or more snappers in approaching an atherina and retreating from it is that which appears in the record as "hesitation."

Early in a series many snappers rushed toward each tentacled red as it was thrown. Later in the series the number of snappers that responded by a rush grew progressively less, until toward the end of the series no snappers rushed forward when a tentacled red was thrown (evidence that the splash of the falling atherina is not a sufficient stimulus to cause the rapid approach of the snappers). The atherinas that were taken late in the red series were taken by the few snappers that happened to be nearest the point at which the fish struck the surface of the water. There was no general rush toward that point. The nearest snappers approached slowly and behaved in the manner already described. In short, the extent to which the individuals of the colony take part in the rush at any atherina appears to be determined by the behavior of those snappers that happen to be nearest the atherina when it strikes the water. If these nearest snappers rush vigorously there is general participation by the other individuals of the colony. If the nearest individuals approach more slowly, no such general participation takes place. A localized stimulus applied to one of the higher animals may, if weak, produce only localized response, but may, if strong, throw the entire organism into vigorous response. Similarly the vigor with which a colony of snappers responds to an atherina appears to depend on the extent to which the atherina serves as a stimulus to the individuals nearest to it.

(*c*) *Formalin reds following formalin tentacled reds.*—These were treated precisely like tentacled reds. Probably the snappers would have behaved no differently had all the reds been tentacled.

(*d*) *Formalin normals following formalin reds* (*tentacled or untentacled*).—The behavior of the snappers is best shown by an extract from my notes on series I. "The change in the behavior of the snappers was most marked. All of them rushed at once at each fish, so that the water fairly boiled. A moment earlier very few snappers had paid any attention to the reds and those that were taken were taken usually by the snapper that happened to be near." Sometimes when a change is made from reds to formalin normals the first few of these are taken by the nearest snappers and with slight hesitation. This hesitation rapidly disappears as more normals are thrown, and the rushes quickly become as vigorous as possible and are participated in by the whole colony. The increasing vigor with which the nearest snappers respond to successive atherinas makes itself rapidly felt in the rest of the colony.

Experiment 33.—As a control on experiment 32, in which the laboratory colony was used, the following experiment was tried on July 19, 1907, at 1^h 36^m p. m., on the west lighthouse colony, which was without experience of tentacled fish. Atherinas were offered as follows: (1) 12 formalin normals; (2) 44 formalin reds; (3) 30 formalin tentacled reds; (4) 30 formalin normals. All were taken at once without hesitation. No difference

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could be observed in the way in which red and white fish were taken by individual snappers or by the colony as a whole. Absence of hesitation in taking tentacled fish is attributable in the beginning to inexperience. That 30 tentacled fish should be so taken is no doubt due to hunger, since this colony had received less food than any other. The hesitation and refusal shown toward red by the laboratory colony is therefore attributable to experience gained during experiment 32. It is neither instinctive nor the result of a previously formed habit.

In 1905 an experiment was carried out differing from that described in the present section only in that the atherinas used were fresh, not preserved in formalin. Excluding some very brief preliminary trials the experiment of 1905 extended over but a single day. Between 9^h 48^m and 3^h 11^m p. m. there were fed to the laboratory colony of about 100 snappers 117 fresh tentacled red atherinas, divided into lots of from 8 to 20, offered at intervals of 30 to 60 minutes; 20 of these, including the last 8, remained untaken, although normal fish were taken readily at all times. The experiment of 1907 is an extension and confirmation of that of 1905.

The results of these experiments may now be briefly stated as follows:

> When red atherinas, rendered unpalatable by attaching to each a part of a tentacle of *Cassiopea,* are offered to a colony of gray snappers, they are at first taken instantly, later taken after the lapse of a longer or shorter time, and finally refused. In 1907 (experiment 32) the final refusal resulted (omitting series II) from feeding to about 150 snappers, 238 formalin tentacled red atherinas, of which 178 were taken and 60 refused. The feeding required 1 hour and 25 minutes, divided into 2 periods of 35 and 50 minutes, separated by an interval of 3 days. In this time there was an average of but little more than one unpalatable atherina taken for each snapper. This sufficed to form for the snappers an association between red and the quality or qualities which rendered the atherinas unpalatable of such a sort that formalin red atherinas were thereafter refused. Formalin red atherinas were refused even when not tentacled, while formalin normal atherinas (uncolored) were taken whether tentacled or not, hence the association is between color and the quality which renders the atherinas unpalatable, not between the form of the tentacled atherinas and that quality. In a second colony of snappers formalin red atherinas were taken readily, in considerable numbers (experiment 33) whether tentacled or not, hence their refusal by the first colony can not be attributed to an instinctive or habitual avoidance of red. Their acceptance by the first colony at the beginning of experiment 32 points to the same conclusion.
>
> The statement seems therefore warranted that in experiment 32 the color came to have for the snappers a warning meaning. A warning color was artificially established. This result was reached in spite of the fact that atherina is the normal food of the gray snapper at the time of year at which the experiments were made. By changing the color of this food and rendering it unpalatable the

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natural, positive response of the snappers toward it was inhibited. This positive response, in so far as it involves the taking of small, near, possible-food objects, is doubtless instinctive; in so far as it involves taking the specific food atherina it is habitual. Had the food offered been such that the snappers had had no previous experience of it, their positive response would have been instinctive only. To inhibit such a general instinctive response requires, as shown elsewhere in this paper (p. 307), a much smaller number of experiences than are necessary to inhibit a response that has become habitual. That an habitual response, toward a particular food commonly present in the environment should be as readily inhibited as in experiment 32 was unexpected and shows a high degree of modifiability in the behavior of the snappers.

VII. THE RETENTION OF THE RED-UNPALATABILITY WARNING ASSOCIATION IN THE GRAY SNAPPERS (MEMORY).

The color red had come to have a warning significance for the gray snappers as a result of their experience with unpalatable red atherinas—an experience which closed on July 19, 1907. This colony was not afterwards offered red atherinas, except at the time indicated below and for the purpose of testing the retention of the red-unpalatability association. On July 23 the colony was fed from 200 to 300 formalin atherinas, newly rinsed in seawater to remove the formalin. These were taken, but many of them were afterwards ejected and lay on the bottom unnoticed. On July 24 an attempt was made to feed these snappers on formalin blue atherinas, but after taking 30 or 40 they began to eject them and would then take no more. On July 26 the colony took 21 out of 30 blue and yellow formalin atherinas offered them.

On July 27, 8 days after the red warning association had been established, I tried all the morning to get the snappers of this colony to take formalin red atherinas (untentacled). They took a few very slowly and then stopped. They took formalin normals more readily and also took blue, but if red was offered immediately after blue or white, it was, even then, taken very slowly. Apparently the snappers still retained the red unpalatability association. The red used was a cardinal red—much purer than the red used in the association experiments.

On August 8, 20 days after the close of the association experiment with formalin tentacled red atherinas, the last attempt was made to feed the laboratory colony on red fish. All the red and blue and yellow atherinas used had been removed from formalin, washed and stained some 10 days before, and had since laid in a moist atmosphere, so that the last trace of formalin had probably evaporated from them. Formalin blue atherinas were first thrown and 4 or 5 of these were taken very carefully. Red was then thrown. Some of both blue and red sank, others floated. ***The reds remained entirely untouched,*** even while they sank among the snappers and

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lay on the bottom. They were not even snapped at or closely examined; in fact they excited no visible interest. Formalin normals (uncolored) were then taken directly from 2 per cent formalin, rinsed, and thrown while still saturated with formalin. They were taken at once, and about 20 were thus taken. Additional reds and some yellows were then offered, but remained practically unnoticed. The stimulus of an immediately preceding feeding on white did not result in the taking of red or yellow.

The behavior of the snappers showed quite conclusively their avoidance of red, which was even more marked than immediately after the establishment of the red-unpalatability association. At that time and also on July 27 an occasional red fish was taken, but on August 8 they remained not only untaken, but appeared to excite no interest.

Although the snappers refused red on August 8 they also refused yellow, while they took blue less readily than before. The warning meaning conveyed thus appears to have been transferred from the red to the yellow, and to a less extent to the blue. Probably atherinas of all colors would have been avoided, and possibly in proportion to the likeness of the respective colors to red. Nevertheless formalin normal atherinas (white) were taken, apparently as readily as ever.

The facts stated in this section seem to me to warrant the conclusion that the red-unpalatability association established on July 19 was still effective on August 8. The associative memory of the snapper has at least this duration. I left the island on my return north on that day.

VIII. RESULTS OF FEEDING THE LABORATORY COLONY OF GRAY SNAPPERS ON CONSPICUOUSLY COLORED CORAL-REEF FISH.

In the preceding sections of this paper evidence is given to show that the gray snapper distinguishes colors, forms with great rapidity associations involving color discrimination, and retains these associations for a considerable time. It has been further shown that it is possible, in a short time, to establish in the gray snapper a warning-color association, of such a sort that its natural prey is protected from attacks when artificially warningly colored. All this lends support to the theory of warning coloration as applied to coral-reef fishes, yet it remains to be learned by experiment whether any of these fish are actually protected from the attacks of the gray snapper by the assumed combination of conspicuous coloration with unpalatability. To test this assumption as many as possible of the coral-reef fishes were collected and fed to the Laboratory colony of snappers. These fish were usually thrown living from the dock, so that they fell with a splash into the water near the snappers. A few were slipped in quietly near the shore, so that, as they swam seaward, their approach to the snappers was more normal. A few of the fish were dead when offered to the snappers, but most of them were very active and made every effort to escape. A few individuals of *Adubefduf marginatus* were rendered immobile by pithing.

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Fig. 10.

Fig. 11.

Fig. 10. Group of large coral-reef fishes in front of branching gorgonians and sea fan, *Rhipidogorgia*.

Fig. 11. Grup of large coral-reef fishes, chiefly *Hæmulon sciurus*. Purple sea fan, *Rhipidogorgia*, at left.

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The results of these feeding experiments are shown in table 13, which also includes one amphibian. The fishes fed were, with one exception (*Chætodon ocellatus*), small enough to be taken by the snappers. Adult individuals of the larger species would have been protected by their size. The salient features of the coloration are given in table 13. For details the reader is referred to systematic treatises (Jordan and Evermann, 1896; Evermann and Marsh, 1900). The color and patterns given in the table are those of the fish seen by the writer in their natural habitat at a little distance, as the fish appear to the snappers. The descriptions have been checked by comparison with captured fish. Preserved fish or those in aquaria (upon which systematic descriptions are usually based) are less brilliantly colored. Of the species listed, only *Sparisoma flavescens* is unquestionably protectively colored, though *Caranx crysos* may be so. The others are in varying degrees conspicuous. *Iridio bivittatus* (plate 4, fig. 7) and the two species of *Thalassoma* vary considerably. While less conspicuous than the others they are to my eye conspicuous. Even casual observation of the remaining species in their natural habitat shows that they are highly conspicuous. Black is a very common color; bright orange and bright yellow are common. Bright metallic blue and green are also common. Scarlet is not rare. All these colors are in strong contrast to those of the reefs. Not only are the colors conspicuous, but they are combined in patterns of contrasting colors. Black and white, black and yellow, or black, white, and yellow in alternating bands or stripes are frequent patterns (*Abudefduf marginatus,* plate 1; *Iridio bivittatus,* plate 4, fig. 7; *Lutianus griseus* juv.; *Chætodon ocellatus,* plate 3, fig. 5; *Chætodon capistratus,* plate 3, fig. 6; *Anisotremus virginicus* juv.; *Pomacanthus arcuatus* juv.; *Angelichthys ciliaris; Eques pulcher*).

Light metallic blue is found alternating in stripes or bands with blue so dark as to be seemingly black (*Elacatinus oceanops,* plate 4, fig. 8), and with these is sometimes associated a metallic green (*Thalassoma bifaciatum*). Orange may be combined with metallic blue or black so that each covers uninterruptably about half the surface of the fish (*Pomacentrus leucostictus, Pomacentrus planifrons*) or yellow and blue may occur in alternating stripes (*Hæmulon sciurus, Hæmulon flavolineatum,* plate 2, fig. 3). Scarlet may cover the whole surface or be combined with black (*Amia* (*Apogon*) *sellicauda*). A uniform black is common (*Pomacentrus leucostictus* at times, *Hepatus hepatus* juv., plate 5, fig. 10, at a little distance).

The colors and patterns are those typical of warningly-colored insects (*cf.* Poulton, 1887, for a list of such colors in insects). They make their possessor conspicuous in its normal environment (see plates 1 to 5). When the coral-reef fish are seen by an observer in air he looks through the surface film of the water and sees the fish usually in sharp contrast against the gray-white sand or rock. It seemed to me worth while to find out whether the fish are equally conspicuous when seen by one beneath the sur-

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face of the water, when seen as their enemies see them. They are then viewed at a different angle. They appear at times against the reef or bottom, at times against the totally reflecting surface film, and at other times against the blue translucence of the more distant water. I have been able to assure myself of the conspicuousness of the fish under these circumstances by two methods. (1) By the use of a reflecting water-glass,[1] I have succeeded, without using a diver's suit, in seeing fish as they appear to other fish. (2) By means of a submerged camera (Reighard, 1908) I have photographed them while they were engaged in their usual activities in their normal environment. Several of these photographs are reproduced in plates 1 to 5, and are sufficiently described in the explanations of the plates. They show certain of these fish as they appear to a submerged observer and seem to me to afford a sufficient demonstration of their conspicuousness. (For further evidence see the plates in Evermann and Marsh, 1902; Jordan and Evermann, 1905; Jordan and Seale, 1906; and Saville-Kent, 1893.)

Many of these fish are rendered still more conspicuous by their form and movements. The great compression of the body (*Chætodon,* plate 3; *Pomacanthus, Angelichthys, Hepatus,* plate 3, fig. 5; plate 5) exposes to view a greater surface which may be further increased by the expansion of the dorsal and anal fins. The movements of the same fish are peculiarly slow and erratic and suggest those of a butterfly on the wing. This peculiarity arises from the use of the pectoral fins rather than the caudal in ordinary progressive movements. The caudal appears to be held in reserve for emergencies, as when the fish are forced to flee to shelter. This erratic, jerky method of locomotion by means of the pectorals is not confined to forms with compressed bodies and expanded fins, but is found also in all the Labridæ observed (*Thalassoma, Iridio, Sparisoma, Scarus, et al.*).

[1] This is a rectangular box of galvanized iron, 2 feet long and with ends 6 by 8 inches. In the interior of the box at each end is a mirror firmly fixed in a metallic setting and placed at an angle of 45° with the long axis of the box. The reflecting faces of the two mirrors are consequently parallel and they are directed toward each other. One end is heavily weighted with lead, so that when placed in water the box floats in an upright position with about 10 inches of the upper end projecting above the surface. Opposite the lower mirror is an opening 6 by 8 inches filled with plate glass bedded in aquarium cement. Opposite the upper mirror are 2 tubes soldered to openings in the side of the box and so spaced that the observer may look through them at the upper mirror. The tubes are lined with chamois skin and so constructed that the objective ends of a pair of field glasses may be inserted into them and firmly clamped in place. A handle on either side of the box enables it to be held steady. The observer, while wading, holds the box in front of him with the lower end immersed. He may then see objects beneath the surface reflected in the two mirrors, just as they would appear to him if his head were beneath the surface. In using this apparatus I finally dispensed with the field glasses, chiefly because I was able to get so near the fish that their use was unnecessary, but partly because the double images formed by the glass mirrors interfered somewhat with their use. The apparatus would be more efficient if double images were avoided by the use of metallic mirrors. These could be kept from tarnishing by sealing the box hermetically by means of glass plates cemented over the inner ends of the tubes for the eyes. With such an apparatus field glasses could be used and, within the limits set by the opacity of the water, the fish could be studied with them as birds are studied in air.

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TABLE 13.—*Result of feeding 22 species of teleostean fishes and one amphibian to the Laboratory colony of gray snappers in July, 1905, and July, 1907.*†

Serial No.	Name.	Length.	No. fed.	How fed.	Coloration and armature.	Result.
		Inches.				
1	Abudefduf marginatus.	1 to 2	11	4 living, 7 with spinal cord cut, from dock.	Yellow and black banded.....	2 living taken, 3 living escaped, 6 pithed taken.
2	Angelichthys (Holocanthus) ciliaris.	5	1	Dead from dock.	Body chiefly bright blue, fins chiefly bright yellow, *preopercular spines.*	Taken at once.
3	Amia sellicauda.*	1.5 to 3.5	2	Living, from dock.	Scarlet, 2 black spots.....	Taken at once.
4	Anisotremus virginicus.	1 to 2	2	Living, from dock.	Yellow, with 2 black stripes, black caudal spot.	1 taken after short pursuit, 1 immediately.
5	Caranx crysos...	2.5	2	Living, from shore.	Silvery, yellow stripe.....	1 taken at once, 1 escaped.
6	Chætodon capistratus.	1.75	1	Living, from dock.	White, black bands and black spot; *large dorsal and anal spines.*	Taken at once.
7	Chætodon ocellatus.	4	1	Living, from dock.	Silvery ground, 2 wide black bands. Fins yellow in part. *Large dorsal and anal spines.*	Attacked, but escaped.
8	Chylomycterus schœpfi.	2 to 4	4	3 living, 1 dead, from dock.	Greenish, heavy black stripes; *body armed with spines.*	2 fishes taken, 2 and 3 inches long; 2 fishes escaped, 3 and 5 inches long.
9	Echineis naucrates.	6	1	Living, from dock.	Broad stripes, nearly black and white.	Taken at once.
10	Elacatinus oceanops.	2	2	Living, from dock.	Broad light and blue-black stripes.	1 escaped, 1 taken at once.
11	Eques pulcher...	2 5	1	Living, from dock.	Black and white conspicuous stripes.	Taken at once.
12	Hæmulon sciurus.	3.5 to 4	2	Living, from dock.	Blue and yellow stripes	Taken at once
13	Hæmulon flavolineatum.	2.5	2	1 dead, 1 living, from dock.	Blue and yellow stripes	Taken at once.
14	Hepatus hepatus.	3 to 4.5	4	Living, from dock.	Black; *lancet on caudal peduncle.*	Taken at once.
15	Iridio (Halichœres) bivittatus.	3 to 8	11	Living, from dock.	Gray, dorsal line and sides with broad dark brown stripes.	Taken at once.
16	Lutianus griseus, *juv.*	2	3	Living, from dock	Yellow-and-black banded	Taken at once.
17	Pomacentrus leucostictus.	2.5 to 4	12	8 dead, 4 living, from dock.	Half orange, half blue or black.....	Taken at once.
18	Pomacentrus leucostictus.	2.5 to 4	10	2 dead, 8 living, from dock.	All black	Taken at once.
19	Pomacentrus planifrons.	2	2	Dead, from dock.	Half orange, half blue or black.....	Taken at once.
20	Pomacanthus arcuatus.	1.25	1	Living, from dock.	Black, 5 conspicuous yellow bands, blue spots. *Preopercular spine.*	Taken slowly.
21	Sparisoma flavescens.	2.25	1	Living, from shore.	Mottled, olive and brown (protective colors).	Taken at once.
22	Thalassoma bifasciatum.	4 to 6	4	2 living, 2 dead, from dock.	Blue head, green body, black band between.	Taken at once.
23	Thalassoma nitidum	4 to 6	13	9 living, 4 dead, from dock.	Very variable, usually green with lateral purple stripe.	Taken at once.
24	Diemyctilus viridescens.	4	1	Living, from dock.	Red.....	Taken at once.
			94			

* 2 living specimens fed to a goby in an aquarium were at once taken.
† The authorities for the scientific names in the table are to be found in Jordan and Thompson (1905). They are here omitted through lack of space.

Table 13 shows that with few exceptions these conspicuous fish were at once taken by the snappers. Some of them were taken in spite of possessing both conspicuousness and unpleasant atributes. Thus *Pomacanthus* has a formidable spine on the preopercle, while *Angelichthys* has this and smaller spines besides. *Chætodon* has strong, erectile spines at the front of dorsal and anal. *Chylomycterus* inflates itself when disturbed and thus erects the many strong spines scattered over the body. *Hepatus* is armed with the

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well-known and formidable lancet at the base of the tail (plate 3, fig. 5; plate 5, fig. 10). These are all weapons which the fish habitually use. There is no evidence that the color of any of the species afforded them the least protection against the snappers. These fish, with the exception of *Caranx, Chylomycterus,* and *Leptechineis,* are reef-fish. The snappers which frequent the inner reefs are familiar with them; they are familiar with the snappers. That their colors or patterns have no warning significance for the snappers is shown by the following facts:

(*a*) The snappers took them at once. They showed no trace of the hesitation or refusal shown, after experience, toward tentacled red atherinas.

(*b*) The fish attempted to escape, sometimes toward the shore, sometimes toward some other near shelter, such as is afforded by the spiles of the dock or by the floating live-boxes beneath it. In this respect their behavior contrasts with that of many typical, warningly-colored animals (*e. g.*, the skunk and "Belt's frog," Belt, 1874), which do not flee from their enemies, but depend for protection on their color.

The fish which escaped were either speedy and not conspicuous, or were hindered rather than helped by their conspicuousness. The following details of these escapes illustrate this:

(*a*) *Caranx crysos* is silvery and yellow, and not conspicuous when seen on the yellow-white sand. One individual, 2.5 inches long, was released 2 or 3 feet from shore. It was pursued by snappers and fled along shore as near as possible to the water's edge. It was several times captured with a net and again released near the snappers, but each time it behaved in the same way and finally escaped by following the shore. A second individual, thrown from shore to a distance of 6 or 8 feet, was at once taken.

(*b*) *Chætodon ocellatus* (plate 3, fig. 5).—An individual 5 inches long was thrown from the dock after the snappers had been brought together by feeding them several atherinas. It was at once viciously attacked by a large number of snappers together, and was lost to sight for an instant. As the snappers separated, the *Chætodon* was seen apparently uninjured and with its spines fully erected. It immediately started seaward and was not further molested. An individual 1.75 inches long, of a rather less conspicuous species (*C. capistratus,* plate 3, fig. 6), was at once taken. The *C. ocellatus,* 4 inches long, was about 4 inches deep from tip of longest dorsal spines to tip of longest anal spine. Such a fish is clearly protected by its size and armature, but not by its coloration, while a smaller individual of a closely related species (*C. capistratus*), conspicuous and provided with means of defense, is readily taken.

(*c*) *Chylomycterus schœpfi.*—(1) A specimen 3 inches long was thrown from the dock. It swam vigorously seaward at the surface, followed by a dozen snappers, which swam about below, approaching and receding. It was finally lost to sight and not taken.

(2) An individual about 5 inches long was thrown. It swam toward shore and was picked up and thrown farther seaward. The snappers collected beneath it and it inflated itself at sight of them, so far as could be seen without being touched by them. It then deflated itself and swam more rapidly so near the surface that the movements of its pectorals disturbed the

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surface water. Several times it was seized by the snappers and again released. It could not be seen whether it again inflated itself, but it was finally lost to sight seaward and probably escaped.

(3) An individual 3 inches long was thrown outside the dock. The snappers followed it for 5 or 6 rods, swimming below it and watching it, but did not seize it. When it had gone out over the dark vegetation-covered bottom, I followed in a row boat. It was swimming at the surface, making with the pectorals a little eddy visible at a considerable distance. It moved so slowly that a 16-foot dinghy could be brought to it by paddling stern foremost with a single oar. Nevertheless I had difficulty in capturing it in a small tin can, because, when approached, it changed its course and dodged about. It was finally captured and thrown from the dock on the shore side. It was already inflated. The short tail, projecting like the neck of a jug from the spherical body, was seemingly the only part of the fish that could be seized. After a moment's hesitation the fish was taken by the tail by an unusually large snapper. He took it to the bottom and mauled it back and forth there as though to force it into his mouth or burst it. He finally lost his hold on it and a second fish seized it by the tail. It passed then to a third and a fourth and each in turn mauled it on the bottom. The fourth fish finally forced it into his mouth and it disappeared.

(4) An individual a little less than 3 inches long was thrown dead from the dock and was at once taken. It was carried 5 or 6 rods down the shore, apparently dropped, and then picked up by another fish. A careful search failed to find it, and it was recorded as finally taken.

Chylomycterus is an occasional visitor in this region and does not occur normally on the reefs, but is often found in the open water in considerable numbers. It is conspicuous in open water. On account of its relative unfamiliarity it appeared to offer a new problem to most of the snappers, a problem involving erratic movement, together with inflation of a heavily-spined body. The problem was nevertheless speedily solved. In the case of No. 3 a single large snapper, possibly with previous experience of *Chylomycterus,* led in the solution; the others quickly followed. Conspicuousness was here a disadvantage.

(*d*) *Abudefduf marginatus.*—This very conspicuous fish is often found with the snappers when full grown. Its yellow and black bands suggest a hornet (see plate 1, figs. 1 and 2). It is deep-bodied, but its dorsal and anal spines are relatively weak (*cf. Chætodon*). It swims slowly, but is very agile, as shown by the following experiences: Two young individuals, 0.5 inch and 1.5 inches long, were placed in a cylindrical aquarium 7.5 inches in diameter and could then be captured only with great difficulty by the use of a conical net with a 4-inch opening. Two young *Lutianus griseus* about 1.66 inches long could be readily picked up from the same aquarium with the same net. It is exceedingly difficult to capture *Adudefduf* with a net 3 feet in diameter in open water. It usually escapes over the rim. Eleven individuals were thrown from the dock to the snappers, 4 of these being alive and active. The results were as follows:

(1) Very active, was taken at once.

(2) Went about 15 feet pursued by snappers, but finally reached one of the live-boxes and was left unmolested.

(3) Was pursued by snappers which came within 8 or 10 inches of it. It swam to a spile underneath the dock and was left unmolested.

(4) Swam to the live-box without being pursued.

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The 3 individuals which escaped joined others of their species which had been for some days living apparently unmolested against the flat bottom and sides of a large, floating live-box. This little group of perhaps a dozen small *Abudefduf* was within a few feet of 100 or more voracious snappers. They were never seen to go more than a foot or two from the surface of the box when feeding. When approached they retreated close to the box, which was smooth on the outside and had no crannies in which they could find shelter. The snappers were never seen to attempt the difficult task of capturing one of these agile little fish against the smooth, hard surface of the box. Not their coloration, but nearness to a large, hard surface protected them.

(5) Was nearly dead when thrown and was at once taken. The remaining 6 *Abudefduf* were made immobile by cutting the spinal cord.

(6) and (7) Thrown in the usual way. They were not at first noticed, but as they sank and made no effort to escape, they were seized.

(8) (9) (10) and (11) Offered to the snappers in the following manner: Bread crumbs were thrown to the living *Abudefduf* at the side of the live-box. They fed on these at and near the surface, but did not venture to follow them as they sank. Beneath the *Abudefduf* the snappers assembled to feed on the sinking bread crumbs. The immobile *Abudefduf* were dropped one at a time past the edge of the live-box, so that they fell among the living ones, which were only 2 or 3 feet above the snappers. As the first immobile (No. 8) *Abudefduf* sank it was followed for a foot or so by one or two living individuals. The snappers gave no heed to either. The living fish returned to the surface, the motionless one sank, still unheeded, among the snappers. When it had reached the bottom and lain there for a moment it was quickly seized. (9) (10) (11) were thrown in precisely the same way as (8), and with the same result.

Clearly the *Abudefduf* near the live-box are treated by the snappers as inaccessible, while individuals of the same species at a distance from the live-box are eagerly pursued and often captured. Immobile *Abudefduf* that sink from the live-box group among the snappers are taken only after a short time, time enough to bring to the snappers a perception of their distinctness from the immune live-box group.

(*e*) *Elacatinus oceanops*.—This slender fish, 1.5 to 4 inches long, is found on the surfaces of the massive coral (*Orbicella*), close pressed to the living polyps. I have found it fully exposed, not "endeavoring to shelter itself in bottom of grooves," as stated by Jordan and Thompson (1905). In this position, where it is conspicuous by reason of its strongly contrasted stripes, it is shown in plate 4, fig. 8. When dislodged it takes a zigzag course to a new resting-place, as described by Jordan (1904). With the greatest difficulty it may be captured from the coral with a hand net.

Two individuals were thrown from the dock to the snappers. The first was pursued, but went at once toward a spile beneath the dock. It was lost to view, but later found clinging to the spile. A second individual thrown in further from the dock was at once snapped up. Here, as in the case of *Abudefduf*, coloration appears to be no protection, but erratic movement aids escape, and nearness to a large, hard surface affords protection, more effective, perhaps, in the case of *Elacatinus*, because of the nettle-cells of the coral polyp to which the fish clings.

The case of *Leptechineis naucrates* is of interest in connection with that

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of *Abudefduf*. Its broad contrasting stripes render it conspicuous. When in its natural position, attached to the body of a shark by the sucker on the top of its head, it is not molested by the snappers. An individual 6 inches long was thrown from the dock and at once taken by the snappers. Its coloration gave it no protection. Just as the snappers treat *Abudefduf* and *Elacatinus* as accessible when not close to a massive coral or large hard surface, so they treat *Leptechineis* as accessible when detached from its host.

The wholly unfamiliar bright red salamander *Diemyctylus viridescens*[1] was taken with no trace of hesitation, and thus is illustrated again the failure of a warning color to afford protection.

The results of the feeding experiments may be briefly summarized as follows:

Gray snappers attempted to capture all the 22 species of fish and 1 amphibian thrown to them. They actually took all the species but one (Chætodon ocellatus), which escaped on account of its large size and defensive armor. No hesitation was shown in seizing any of the fish offered, except in the case of the larger individuals of Chylomycterus schœpfi, which are formidable by reason of their erratic movements, power of inflation, and defensive spines, and are probably new to most of the snappers. The species taken were of a variety of colors and color patterns and were nearly all conspicuous. They included the colors and patterns considered as typically warning. In Angelichthys, Chætodon, Chylomycterus, Hepatus, and Pomacanthus conspicuousness is combined with unpleasant attributes in the form of defensive spines, the typical warning combination, yet these fish were all instantly taken.

Individuals of certain species escaped from the pursuing snappers, (a) because of inconspicuousness combined with speed (Caranx crysos); (b) because of erratic movement combined with power of inflation, size, and defensive spines (Chylomycterus schœpfi); (c) because of erratic flight to a near object with large, hard surfaces, against which a small agile fish is practically inaccessible (Abudefduf marginatus, Elacatinus oceanops). The escape of these individuals was therefore not due to their conspicuous coloration, but was rather in spite of it.

IX. THE RAPIDITY AND NICETY OF THE ADJUSTMENT OF THE GRAY SNAPPER TO ITS FOOD.

In this section there are brought together a few instances of behavior adjustment which appear to bear on the theory of warning coloration.

On July 14, 1905, there were fed to the laboratory colony of gray snappers 151 atherinas, the last 28 of which were blue. Immediately afterward there were offered 3 blue atherina-shaped pieces of the arms of the medusa *Cassiopea xamachana*. These pieces induced no reaction whatever in the snappers, although they greatly resembled a blue atherina which was thrown immediately before them and at once taken. When it was clear that the fish would not take the blue cassiopea pieces, they were offered a composite of

[1] I am indebted for this specimen to Mr. Davenport Hooker.

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atherina and cassiopea, made by shaping the cassiopea to the form of an atherina body and sewing to this the head and tail of an atherina. The whole was blue and at a little distance hardly to be distinguished from an atherina. It was at once taken.

The next day (July 15) after a previous feeding of but 18 uncolored atherinas, 2 pieces of the rim of cassiopea were stained blue and thrown to the snappers after a single blue atherina. The pieces of cassiopea were about 1 inch wide and 3 inches long. One continued to pulsate; the other did not. Both were at once taken.

Experiment 34: Shortly afterward pieces of the arms of cassiopea were trimmed as near as possible to the size and form of atherina. They were

TABLE 14.—*Behavior of the laboratory colony of gray snappers toward blue and red atherinas and toward blue and red atherina-shaped cassiopea arms, when offered, in alternation after normal atherinas.*

[*na* = normal atherina; *ba* = blue atherina; *ra* = red atherina; *bc* = blue cassiopea; *rc* = red cassiopea.]

July 15, 1905.	Serial No.	Object offered.	Taken.	Taken and rejected.	Refused.
Beginning 12 m.	1	*na*	×		
	2	*na*	×		
	3	*na*	×		
	4	*ba*	×		
	5	*bc*		×	
	6	*ba*	×		
	7	*bc*		×	
	8	*ba*	×		
	9	*bc*		×	
	10	*ba*	×		
	11	*bc*			×
	12	*ba*	×		
	13	*bc*		×	
	14	*ba*	×		
	15	*bc*			×
	16	*ba*	×		
	17	*bc*			×
Per cent, cassiopea.				57	43

July 16, 1905.	Serial No.	Object offered.	Taken.	Taken and rejected.	Refused.
Beginning 11 a. m.	1	*na*	×		
	2	*na*	×		
	3	*na*	×		
	4	*ba*	×		
	5	*bc*			×
	6	*ba*	×		
	7	*bc*			×
	8	*ba*	×		
	9	*bc*		×	
	10	*ba*	×		
	11	*bc*			×
	12	*ba*	×		
	13	*bc*			×
	14	*ba*	×		
	15	*bc*			×
	16	*ba*	×		
	17	*bc*			×
	18	*ba*	×		
	19	*bc*			×

Beginning 1h30m p. m.	1	*na*	×		
	2	*na*	×		
	3	*na*	×		
	4	*ba*	×		
	5	*bc*			×
	6	*ba*	×		
	7	*bc*			×
	8	*ba*	×		
	9	*bc*			×
	10	*ba*	×		
	11	*bc*		×	
	12	*ba*	×		
	13	*bc*			×
	14	*ba*	×		
	15	*bc*			×
	16	*ba*	×		
	17	*bc*			×
	18	*ba*	×		
	19	*bc*			×
Per cent, cassiopea.				12.5	87.5

Beginning 11h45m a. m.	1	*na*	×		
	2	*na*	×		
	3	*na*	×		
	4	*ba*	×		
	5	*bc*			×
	6	*ba*	×		
	7	*bc*			×
	8	*ba*	×		
	9	*bc*			×
	10	*ba*	×		
	11	*bc*			×
	12	*ra*	×		
	13	*rc*			×
	14	*ra*	×		
	15	*rc*			×
	16	*ra*	×		
	17	*rc*			×
	18	*ra*	×		
	19	*rc*			×
Per cent, cassiopea.				6.25	93.25

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smooth, jelly-like masses without tentacles or other projections, and on one surface of each the epithelium with its nettle-cells remained intact. These pieces were stained blue and thrown to the Laboratory colony of gray snappers alternately with blue atherinas, in the manner shown in table 14 at the left.

After 3 normal atherinas, 7 blue atherinas and 7 cassiopea pieces were thus thrown at noon. The atherinas were all taken at once; 4 of the cassiopea pieces were taken but rejected, while 3 remained untaken. These 3 sank among the snappers and remained on the bottom. At 1^h 30^m p. m. 8 more blue cassiopea pieces were thrown, alternately with blue atherinas and following 3 normal atherinas. The atherinas were again all taken, while 7 of the 8 cassiopea pieces were refused and 1 was taken and then rejected. On the following day (July 16) at 11 a. m. blue cassiopea and blue atherinas were again offered, 8 of each, and with the result that but 1 cassiopea piece was taken and this was afterward rejected (table 14, at right). At times the snappers showed no reaction toward a cassiopea piece. At other times they swam slowly toward the piece as though to take it, but stopped when within a varying distance, never less than 6 or 8 inches, and then turned away. Usually the movement toward the piece was but 2 or 3 inches; often there was no forward movement. The atherinas, on the other hand, were seized with a rush and unerringly at the first rush. The attempt was repeated forty-five minutes later (at 11^h 45^m a. m.), but with this difference: that after 4 blue atherinas and 4 blue cassiopea pieces had been thrown, the remaining 4 of each thrown were red (table 14, right, below). Both blue and red atherinas were at once taken, but all the cassiopea pieces were refused. Although none of the cassiopea pieces were taken the snappers rushed at the first piece thrown and nearly seized it. They behaved in the same way toward the second and third pieces, but with each succeeding piece their interest lessened, until they paid little attention to the last two or three. In this experiment the atherinas and cassiopea pieces were handled and thrown by different individuals so that there was no transfer of the odor or taste of one to the other.

During the 3 days this colony, consisting at this time of about 100 snappers, actually swallowed 2 pieces of cassiopea and 2 of cassiopea combined with atherina, while they took into the mouth and rejected 6 other cassiopea pieces. In addition to this they examined, without touching, many of the other pieces of cassiopea. As the result of this brief experience the last 13 cassiopea pieces remained untaken, while the percentage taken and rejected declined from 57 at the beginning through 12.5 to 6.25, as shown in table 14. The colony thus adjusted itself with great rapidity to a new possible-food element, of unfamiliar color and form, but with the familiar unpalatable qualities of the medusa.[1] In doing this the individual snappers showed con-

[1] That in this adjustment some of the snappers profited by the experience of others is likely. We have here probably a form of imitation—a following instinct—but the data at hand do not warrant a critical discussion of the subject.

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siderable power of discrimination. The atherinas and cassiopea pieces were much alike. They were identical in color, but differed in details of form and in translucence, as well as in palatability. In spite of their likeness the snappers discriminated accurately between them. That this discrimination was based on form or translucence rather than on color appears from the fact that the snappers were not deceived when red cassiopea was substituted for blue, and from the further fact that they took at once the combined atherina-cassiopea. It is clear that no conspicuous difference, no warning coloration, was necessary to enable the snappers to rapidly differentiate the two sorts of objects.

Experiment 35.—On July 23 two small aquarium jars of uncolored atherinas preserved in formalin were fed to the laboratory colony of snappers. No record was kept of the number fed, but it was estimated to be between 200 and 300—or 2 atherinas to each of the 150 snappers. The atherinas were taken from the 2 per cent formalin, rinsed in sea-water, and thrown at once, while still saturated with the formalin. They were all taken, but very slowly toward the end. Soon snappers were frequently seen swimming about with heads of atherinas projecting from their mouths; 15 minutes later many (probably 50 or 100) atherinas that had been disgorged by the snappers could be seen on the bottom under the dock.

On July 24 blue formalin atherinas were offered to this colony. They were taken very slowly, and after 30 or 40 had been taken, they were refused. Many were then disgorged. In the midst of this feeding of blue atherinas some perfectly fresh uncolored individuals were offered. Some of these still had enough life to wriggle feebly. These were cautiously approached by the snappers, which often jerked back from them, but finally took them. The living fish, while still wriggling, were thus treated by the snappers in a manner wholly unlike that usual to them when fed on fresh atherinas. It was clear that the snappers had retained since the day before an association between the atherinas colored or uncolored and the disagreeable qualities of formalin.

Atherinas are inconspicuous when seen against the surface film or the sand bottom, as the snappers see them. They may be regarded as protectively colored. If all the atherinas about the island were suddenly to become highly unpalatable, I do not doubt that the snappers would learn after a brief experience to let them alone. I do not doubt that they would be effectively protected by unpalatability alone, without the addition to it of a warning coloration—so rapid and so nice is the power of discrimination in the gray snapper. This ability of the snapper to discriminate with nicety has led to its adjustment to all the food elements of its environment. Fragments of a large coral polyp which I threw to them were taken, but at once rejected. Pieces of the arm of a brittle-star were examined and left untouched. Both were inconspicuous. A palinurus, 3 inches long, was at

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once taken. It also is inconspicuous. Medusæ and Ctenophores of various sorts, usually inconspicuous, are not eaten.

We may say by way of summary that the gray snapper discriminates with great rapidity and delicacy between the various possible-food elements of its environment, which are not conspicuously different from each other.

X. GENERAL DISCUSSION OF CONSPICUOUSNESS IN ANIMALS.

THE SIGNIFICANCE OF CONSPICUOUS COLORATION IN CORAL-REEF FISHES.

If the foregoing account is correct the gray snappers, the commonest predaceous fish of the coral reefs, possess all the qualities required by the theory of warning coloration. They distinguish colors, form associations with great readiness, and retain these associations for a considerable time. Presumably other predaceous fish of the region do the like. By these qualities the snappers adjust themselves continually to their environment. Their capacity for behavior adjustment is indeed so great that a familiar disagreeable quality added to their wonted food is enough to render that food immune from their attacks, and this happens after approximately a single experience of taking the food into the mouth (experiment 32, p. 285). An adjustment even more rapid takes place toward food of unfamiliar appearance, but with well-known unpalatable qualities (atherina-shaped colored cassiopea pieces, experiment 34, p. 305). Their capacity for adjustment is such that the snappers have learned all the food possibilities of the environment—what is good for them to eat and what is not. They refuse at sight jelly-fish and brittle-stars, and in spite of the fact that these forms are very inconspicuous, they distinguish them as not good to eat. A warning coloration is quite unnecessary for the protection of these unpalatable forms There can be no doubt that if any animal in the environment of the snappers, whether conspicuous or inconspicuous, should develop highly disagreeable qualities, it would, after a brief experience, be unmolested by them.

When, under quite normal conditions, the gray snappers were given an opportunity to feed on conspicuously colored coral-reef fishes of suitable size they took without hesitation all the species offered them. Most of these 22 species are highly conspicuous fish; several have both conspicuousness and formidable means of defense. That they are greedily taken by the gray snappers and that the fish themselves make every effort to escape are facts which seem to admit of no other interpretation than that their conspicuousness has no warning significance. We must, then, seek some other meaning of the conspicuousness of these fish. Reasons have been already given (p. 263) for the belief that we are not dealing here with sexual selection.

That the conspicuous coral-reef fish are not instances of aggressive resemblance either general or special is evidenced by their conspicuousness, as shown in the photographs (plates 1 to 5, except plate 4, fig. 9). That an aggressive resemblance (enabling them to approach their prey) is unneces-

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sary is due to the nature of their food, which consists, so far as is known, of invertebrates, most of them fixed. This is seen from their mode of feeding by browsing from the surface of the coral rock or from living corals. It is further shown by the tooth structure of many of the forms, a structure adapted for nibbling from hard surfaces and for crushing hard, fixed forms

TABLE 15.—*Stomach contents, so far as recorded, of species of coral-reef fishes known to occur at the Tortugas, Florida.*[1]

Species examined.	No. of fish examined.	Stomach contents.		From notes by writer and Dr. Linton, 1907.
		From Linton, 1907.	From Linton, 1907*a*.	
Abudefduf marginatus (= saxatilis).	10		Vegetable débris.	
Angelichthys (Holocanthus) ciliaris	11		Alimentary canal filled with a red sponge, a few annelids, bryozoa, a small mollusk shell, and seaweed.	
Angelichthys (Holocanthus) isabellita.	1	Alimentary canal filled with gorgonia, sponges, etc.		
Balistes carolinensis	4		Alimentary canal crowded with broken mussel shells, setæ of large annelid.	
Balistes vetula	1		Fragments of adductor muscle of a bivalve mollusk.	
Chætodipterus faber	1	Very long intestine filled with material browsed from the reef, mainly gorgonia and sponges.		
Chætodon ocellatus	2		Algæ.	
Hæmulon flavolineatum.	16		Crustaceans, annelids, green algæ and broken shells	
Hæmulon macrostomum.	(?)	(2) Annelids	Annelids and ophiurians.	
Hæmulon sciurus	35		Crustacea and annelids.	
Hepatus (Teuthis) cœruleus.	4		Broken shells, mainly serpula tubes and small gasteropods, bryozoa, sponge, foraminifera, seaweed and sand.	
Hepatus (Teuthis) hepatus.	5		Ascidian (Botrylloides), algæ, and sand	
Holocentrus ascensionis.	4		Small crustaceans.	
Iridio bivittatus	5		Shells and byssus of mussel, annelid, spine of sea urchin.	
Ocyurus chrysurus (Bloch).	1			1 goose barnacle, 1 isopod, many annelid spines, Ostracoda, bivalve mollusks.
Pomacanthus arcuatus.	2			Compound ascidians, red fibrous sponge, fragments gray calcareous sponge, green pycnogonid, red algæ, conical bryozoan colonies.
Pomacentrus fuscus	.....		Small crustaceans, bryozoa, foraminifera, algæ, sand.	
Scarus (Callyodon) vetula.	4		Stomach and intestine filled with crabs, univalve shells, sea-urchin spines, seaweed, and sand	
Total	108			

[1] Additional notes on stomach contents of fish from Beaufort, North Carolina, of a few species occurring at Tortugas (*Kyphosus sectatrix, Monocanthus hispidus, Chylomycterus schœpfi, Chætodipterus faber*) are to be found in Linton (1905). They are confirmatory of those given in this table, but are not included because, although a reef occurs there, the region is not a typical coral-reef region.

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rather than for holding active prey. The only records of examinations of stomach contents known to the writer are embodied in table 15. This includes 18 species represented by at least 108 individuals and shows the food to include the following fixed or very slow-moving forms: Algæ, ascidians, bryozoa, sea-urchins, gorgonians, mollusks, sponges. The annelids are in one case sedentary or tube-inhabiting forms and are possibly so in all cases. Of active forms, crustacea are mentioned but four times and ophiurians once; both may have been taken after death. The sand is probably adventitious and the foraminifera may have been included in it. The conclusion seems to be warranted that the food of these coral-reef fishes consists of invertebrates, the bulk of it of fixed forms. There appears to be no evidence that any of these aquatic invertebrates discriminate colors (Washburn, 1908, Chapter VII). Aggressive color-resemblance can then afford no advantage to fish approaching such prey and selection could not have operated through the food to hold in check the development of their brilliant colors.

Protective resemblance seems to have been equally unnecessary for the conspicuous coral-reef fishes. Protected by their agility and their nearness to the coral-rock labyrinths, they readily elude their enemies. The method of escape and subsequent behavior of small *Abudefduf marginatus* and of *Elacatinus* related on p. 302 show that these fish are immune from attack when near a large flat surface, whether that surface is or is not clothed with coral polyps. That the conspicuous coral-reef fishes are pursued and captured by the gray snapper when they venture away from the reefs is shown by the feeding experiments already described. One of the fish thus instantly devoured by the snappers was a young *Anisotremus virginicus*, or porkfish, yet I have twice seen this conspicuous fish emerge from crevices in the coral rock and go to a distance of 6 to 8 inches to nibble at the surface of a gray snapper. It avoided the head of the snapper and appeared to be seeking food in the region of the anal opening. Instead of attempting to seize it the snapper lowered the dorsal, wriggled as though annoyed, and then swam away. The instance illustrates the immunity enjoyed by such fish when on the reefs and the recognition by the snapper of their inaccessibility under these circumstances. The gray snappers were never seen to attempt to pursue the conspicuous fish into the recesses of the coral reefs. In the gloom prevailing there the colors of the fish would be indistinguishable and could not then, even should we assume them to be associated with disagreeable qualities, serve to warn their foes. Protective resemblance is unnecessary for such fishes. For them coloration has no selective value. Even were they protectively colored the sharp sight and fine power of discrimination of the snappers would probably enable them to capture the fish at a distance from the reefs, but it is only when they reach a size which renders them immune from attack that they venture to a distance.

Since these fishes, if removed from the reefs, would, on account of their

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conspicuousness, be quickly exterminated, it may be objected that their colors are in fact warning colors, that the reefs with their nettling corals furnish the disagreeable qualities which protect the fish and which correspond to the unpleasant attributes of warningly-colored insects. It may be urged that, just as insectivorous foes, after attacking warningly-colored insects and experiencing their unpleasant qualities, afterward let them alone, so piscivorous fish, after being bumped or stung in their efforts to capture coral-reef fish, subsequently refrain from such efforts. Coral-reef fish, removed from the reefs, are stripped of their disagreeable attributes and are at once attacked. In like manner warningly-colored insects, if deprived of their unpleasant attributes, would doubtless be soon attacked and exterminated. Thus, it may be said, the two cases are quite parallel and the conspicuousness of the coral-reef fish is as much an instance of warning coloration as that of warningly-colored insects, with the difference that the association formed by their enemies is in the case of insects with an unpleasant attribute inherent in the insect, and in the case of coral-reef fish with a similar attribute belonging to their environment. There is a measure of truth in this contention, for no doubt the sight of the reefs "warns" predaceous fish of the futility of pursuing prey into them, and no doubt also the coloration of certain insects may "warn" their foes of their unpalatability. That the coloration of unpalatable insects is unnecessary as a warning and that it has therefore not developed under the action of selection are propositions which are discussed elsewhere in this paper. The evidence that the conspicuousness of coral-reef fish does not warn the gray snapper has been already presented, so that it need be here only added that in any pursuit by enemies, whether outside the reefs or within them, the conspicuousness of these fish is a disadvantage to them. Their capture by the gray snapper can serve only to strengthen in him a mode of behavior which would be correlated in human consciousness with the proposition—"that gaudy morsel is good to eat." A gaudiness which serves to advertise palatability is surely in this case disadvantageous. It could not, therefore, have developed through selection, which, had it acted on these fishes with sufficient intensity, should rather have brought about protective coloration. That this result has not been reached may be due in part to the lack of intensity in the selective process, since selection is held in abeyance by the reefs, but more probably results from the inability of the fishes to vary in the necessary direction.

If the conspicuousness of the coral-reef fish is not necessary in its courtship, and does not serve to warn enemies of unpleasant attributes, and does not aid its possessor in eluding enemies or approaching prey, it can, so far as I can see, and whatever be the physiological uses of the chemical substances involved, have no biological meaning. It has arisen not through selection of any sort, but because the conditions of life permit a suspension of

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selection so far as concerns the color characters of the fish. Selection has neither produced nor perfected the color characters; they have, on the contrary, arisen in the absence of selection and may be regarded as expressions of the individuality of the species unhampered by selection—as expressions of the action of internal factors, possibly orthogenetic.

In the reef environment the chemical composition, temperature, and illumination of the water show a high degree of uniformity both seasonal and regional (Hickson, quoted by Packard, 1902). In this environment many of the fishes that live habitually in the reefs are highly conspicuous on account of their coloration or other characters, while other fishes that live habitually about the reefs but not in them are inconspicuous. Conspicuous coloration can not, then, be attributed to the influence of light, temperature, or chemical composition of the water, which are the same in the reefs and about them (Hickson). Possibly the food of the reef fishes or unknown external factors tend to stimulate in them the development of a brilliant coloration, and this might be experimentally tested. That the environmental factors peculiar to the reefs do not necessarily produce such coloration is shown by *Kyphosus sectatrix*, a reef-fish in the stomach of which Linton (1905) found crabs, lamellibranchs, and vegetable débris. This fish is dull-colored and inconspicuous, yet is found with the conspicuous fish and has like food. But even should it be shown that the reef environment includes factors which tend to produce brilliant colors the many color-patterns characteristic of species would remain unexplained; for the number of color-patterns among coral-reef fish is very great, while the environment is one of great uniformity and the food of the species is little varied.[1] The characteristic colors and patterns I can regard only as due to internal factors, unchecked by the selection which renders them impossible in the immediate neighborhood of the reefs. The reef fauna may include fish conspicuous or not, according to their nature; the water immediately about the reefs can harbor only relatively inconspicuous fish. Nor does it seem to me possible that reef fish could have developed conspicuousness outside the reefs and then sought their shelter (Davenport, 1903, segregation in the fittest environment), for conspicuousness at a distance from the reef shelter would be fatal. On the other hand, inconspicuous fish may have appeared in the reefs and then made their way out from them. *Coral-reef fishes are not conspicuous because they are in the reefs; they are in the reefs because they are conspicuous and can not therefore leave the reefs, and because, being in the reefs and taking the food as they do, there is no reason for their being inconspicuous. The reefs condition their conspicuousness; they are in no sense its cause.*

[1] The conditions resemble those found by Gulick (1905) in the Hawaiian Achatinellidæ, but as my own observations are insufficient to warrant the discussion of *divergent* evolution, I do not here consider Gulick's work.

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HISTORY OF THE THEORY OF WARNING COLORATION.

Darwin, unable to explain by natural selection the conspicuous colors of many animals, suggested the theory of sexual selection, but encountered then a difficulty in certain caterpillars which, though conspicuous, do not show sexual dimorphism. This difficulty he referred to Wallace, who suggested (Wallace, 1867) the ingenious theory to which the term "warning coloration" was later applied. The history of the theory up to the year 1887 is to be found in full in Poulton (1887) and need not be here repeated. It is also to be gathered in part from the later work of Poulton (1890) as well as from Beddard (1892) and Wallace (1891).

Notable contributions of facts in connection with the theory have since been made by Finn (1895, 1896, 1897, 1897*a*), by Marshall and Poulton (1902), and by Pritchett (1903). The observations of Finn are of especial importance, since many of them were made on birds at liberty. Originally applied to the immature stages of Lepidoptera, the theory has been extended to imagos of this group and to other groups of insects, notably to Coleoptera, as well as to various other invertebrate groups. It has now been applied to all the groups of vertebrates. Among mammals the skunk was first instanced by Wallace (1891) and is a classical example. Wallace (1891) and Marshall and Poulton (1902) have cited instances among birds and the latter authors have supported their position by experimental evidence. The striking colors of certain poisonous snakes are commonly cited as examples of warning coloration. Among Amphibia "Mr. Belt's frog" (Belt, 1874, p. 321), and the European *Salamandra maculata* are accorded the places of honor, as striking instances of warning coloration. Among fishes Garstang (quoted by Poulton, 1890, p. 165, footnote) has suggested the black dorsal fin of *Trachinus vipera* as warningly colored. Wallace (1891, p. 266) has added certain coral-reef fishes. Hickson (quoted by Packard, 1904) considers the patches of color about the tail spines of certain surgeon-fishes and similar markings in certain trigger-fishes to be warning in function. Bristol (1903) in a very brief note has suggested a classification of the coloration of coral-reef fish based on its biological significance and has assigned a warning meaning to certain types of coloration. The brevity of Bristol's statement and the absence from it of supporting evidence make it inadvisable to discuss it, but the final paper may well be awaited with great interest.

ANALYSIS OF THE THEORY OF WARNING COLORATION.

The observations in support of the theory of warning coloration are so largely confined to the group of insects that the discussion may, for the moment, be conveniently restricted to this group. If we separate from other matter the observations upon which the theory rests they are, I think, accurately summarized in the following brief statements:

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I. (*a*) *Certain insects are readily eaten by insectivorous vertebrates and these are, with few exceptions, inconspicuous* (protectively colored).

It may be remarked apropos of this statement that it is an obvious necessity. A palatable insect without means of defense could not be conspicuous and exist where persecuted by vertebrate foes. The palatable forms which remain and are accessible to vertebrate foes are therefore those which are inconspicuous in their natural setting.

(*b*) *Other insects are* (*in one or another stage*) *either refused by insectivorous vertebrates or tasted and then rejected or eaten with more or less evident "signs of disgust." These are, with few exceptions, warningly colored.* Insectivorous vertebrates learn by experience to avoid them. (See especially Finn, 1897*a*.)

(*c*) According to the recent observations of Marshall (Marshall and Poulton, 1902) insectivorous invertebrates (mantids, spiders, dragon flies, etc.) do not refuse conspicuous insects, but usually eat them, although Acreinæ are usually refused by spiders. Insectivorous invertebrates need not, therefore, be further considered in discussing the theory of warning colors.

These statements are based chiefly on feeding experiments in which captive vertebrates have been fed upon insects, but without being offered a choice between conspicuous and inconspicuous forms. The results of different observers are not wholly in accord. *Cf.* Poulton (1887) and Marshall and Poulton (1902), with Beddard (1892), and Pritchett (1903). As Finn (1897*a*) has pointed out, experiments should be made on vertebrates at liberty and they should be offered a choice. Those observations of Finn that were carried out in this way are in accord with the statements made above under (*a*) and (*b*), and are the most conclusive known to me. It is highly desirable that there should be further observations of the same sort as well as studies of the stomach contents of insectivorous vertebrates. Nevertheless, the foregoing statements may be provisionally accepted and it is unlikely that future work will essentially modify them.

Upon the observations summarized above certain inferences have been based and these may in turn be conveniently summarized in the following statements:

II. (*a*) *That the conspicuousness of those insects that are provided with means of defense serves not merely to warn insectivorous vertebrates, but is advantageous or necessary for that purpose,* as the insects are thereby protected from attack, while their insectivorous foes are saved unpleasant experiences. To conspicuousness is thus assigned an advantageous or necessary biological function.

(*b*) *That warning coloration has been developed by selection,* through the continued destruction by insectivorous vertebrates of the least conspicuous of the insects provided with means of defense.

These tenets are so obviously a necessary part of the theory of warning

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coloration that they are often implied rather than explicitly stated by writers on the subject. I therefore quote the following detailed statement by Wallace (1891, pp. 242–243) (the italicizing is mine):

> But when they (the Heliconidæ) first arose from some ancestral species or group which, owing to the food of the larva or some other cause, possessed disagreeable juices that caused them to be disliked by the usual enemies of their kind, they were in all probability not very different either in form or coloration from many other butterflies. They would at that time be subject to repeated attacks by insect eaters, and, even if finally rejected, would often receive a fatal injury. Hence arose the necessity of some distinguishing mark, by which the devourers of butterflies in general might learn that these particular butterflies were uneatable; and every variation leading to such distinction, whether by form, color, or mode of flight, was *preserved and accumulated by natural selection,* till the ancestral Heliconidæ became well distinguished from eatable butterflies, and thenceforth comparatively free from persecution.

CRITICISM OF THE THEORY OF WARNING COLORATION.

(*a*) *With reference to tenet II* (*a*) *above.*—Since palatable forms can not be conspicuous and at the same time accessible to their vertebrate foes, it follows that unpalatability must (assuming it to have appeared after insectivorous vertebrates) have arisen among inconspicuous insects and these inconspicuous forms must subsequently have become conspicuous. This accords with the statement of Poulton (1890, p. 176): "it must be remembered that an unpleasant attribute must always appear in advance of the warning color" and also with the existence at the present time of unpalatable insects that are protectively colored (*Mana typica,* Beddard, 1892; *Manestra persicariae,* Beddard, 1892, and many others). That there is no necessary physiological relation between the unpleasant properties of the body juices and conspicuous coloration is shown by the existence of these alleged unpleasant juices in protectively-colored forms, and their absence in certain conspicuous forms. Thus Wallace (1891, p. 254) says: "The eatable butterflies comprise not only brown or white species, but hundreds of Nymphalidæ, Papilionidæ, Lycænidæ, etc., which are gaily colored and of an immense variety of patterns." (See also the table of Beddard, 1892, pp. 164–165.) It is further shown by the coexistence of conspicuous coloration with disagreeable attributes other than unpleasant juices (stings, pricking hairs, Poulton, 1891). The manner in which warning colors are held to have been developed in unpalatable insects is indicated by the above quotation from Wallace.

This mode of origin implies the possession by insectivorous vertebrates of a considerable nicety of discrimination, concerning the existence of which we do not appear to have experimental evidence. But the facts of mimicry seem to afford indirect evidence of well-developed powers of discrimination in insectivorous vertebrates. We have no other explanation of mimicry among Lepidoptera than that afforded by the theory of natural selection, and a careful examination of the evidence on which the theory of mimicry

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rests leaves one impressed with its soundness. The resemblance between mimicked and mimicker have been characterized by Bates as at times "perfectly staggering." Wallace states (1891, p. 245) that "in almost every box of butterflies brought from tropical America by amateurs are to be found some species of the mimicking Pieridæ, Erycinidæ, or moths, and the mimicked Heliconidæ, placed together under the impression that they are the same species. Yet more extraordinary, it sometimes deceives the very insects themselves." The differences between mimicked and mimickers may afford us a measure then of the power of discrimination of insectivorous vertebrates, for according to the theory those mimics which differed noticeably from their models have been continually destroyed by their vertebrate foes until the survivors have come to be so like their models that they can no longer be distinguished from them. Any greater differences must attract the attention of these foes. Insectivorous vertebrates thus show a power of discrimination exceeding that of many amateur collectors.

That the gray snapper possesses some such power of discrimination may be inferred from the experiments already described. Bateson says that the wrasse "finds a shrimp if the least bit exposed, in spite of its protective coloration" (Poulton, 1890, p. 204). If this power be conceded to fishes, insectivorous reptiles, birds, and mammals may well possess at least equal nicety of discrimination. Recognition marks, if they are recognition marks, afford another instance of discriminative power among vertebrates, while protective and aggressive resemblance are quite generally accepted as having arisen through selection which has depended on the powers of discrimination of vertebrate foes.

The theory of warning colors requires us, on the other hand, to assume that these same insectivorous vertebrates possess so little power of discrimination that unpalatable insects need to be marked in conspicuous patterns of contrasting colors. May we not with more reason assert that, if insectivorous vertebrates have pushed the resemblance between mimickers and their models to the point of apparent identity, warning colors are for them quite unnecessary? The ordinary specific differences should suffice to "warn" them of the unpalatability of prospective and familiar insect prey. If this be true warning coloration has no more title to be so called than have other distinctive characters of insects. That it actually serves to "warn" insectivorous vertebrates can not be doubted, but that it is necessary to that end may be seriously questioned.

With reference to tenet II (b) above.—If insectivorous vertebrates possess the nicety of discrimination required by the theories of mimicry and protective resemblance, then it is difficult to see how selection can have produced warning coloration. Selection can no more account for incipient warning coloration than it can account for other incipient characters, for like other characters, warning coloration must have developed to the point

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of utility before selection can have operated on it. As a condition antecedent to selection, incipient warning coloration must have reached a point at which insectivorous vertebrates could distinguish warningly-colored insects from those which did not possess that character. It is conceivable that selection then operated to intensify warning coloration, but can we believe that it carried it to its present stage—far beyond the point at which discrimination must have been easy? Should it not rather have stopped so soon as warningly-colored insects were readily discriminated, long before the present very conspicuous differences had appeared? Are we to believe that when an insectivorous vertebrate encounters together two color varieties of a familiar, unpalatable species which differ slightly in conspicuousness, it will take the less conspicuous and leave the other? Does it seem still further possible that this result will follow if the two varieties are encountered in succession? Should the varieties differ from one another in conspicuousness to the extent of mutations, can one believe that a vertebrate foe with experience of the equal unpalatability of both would take the one and leave the other? Yet this must have been the case if warning colors were perfected by selection. Is it not more probable that if any discrimination occurs, the vertebrate foe would attack the more conspicuous insect because it is less familiar and that his attacks would thus tend to retard the development of conspicuousness rather than to accelerate it?

If warning coloration may be initiated in insects without the aid of selection, as indeed it must be, and if the later stages in its development may not be satisfactorily accounted for by selection, then we need not invoke its aid at all. The entire development of warning coloration may well have been due to the action of the same forces that initiated it. That these forces may be orthogenetic is obvious, but my own work does not seem to afford a sufficient basis for the discussion of this subject. Mayer (1902) has concluded that in butterflies of the genera *Papilio* and *Ornithoptera* and in Hesperidæ the color-patterns have been mainly determined by internal factors (race tendency), not by external influences or natural selection.

A SUBSTITUTE FOR THE THEORY OF WARNING COLORATION.

If the views already expressed concerning the development of conspicuousness in coral-reef fishes are well founded, this character has resulted from the action of internal forces in the absence of counteracting selection. Selection in the direction of protective resemblance has been held in abeyance by the coral-reef habitat which has effectually limited the attacks of predaceous fish. Selection in the direction of aggressive resemblance has not taken place owing to the nature of the food. As a result coloration has developed unhampered by selection and this development has resulted in definite colors and patterns, constant and characteristic of each species. Among these are the colors and patterns typical of warningly-colored insects.

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What has happened with coral-reef fish may well have happened with insects. With them also, with few exceptions, the nature of the food precludes selection in the direction of aggressive resemblance. The development of unpalatability bars in large measure the attacks of vertebrate foes and holds in check selection in the direction of protective resemblance. As a result unpalatable insects have, probably with few exceptions, been free to develop color characters, each according to its kind. This development has, in most cases, resulted in conspicuousness, and to this conspicuousness the term "warning coloration" has been applied.

For the term warning coloration it would, it seems to me, be better to substitute the term *immunity coloration.* If the foregoing account is well founded the so-called warning coloration of insects has not been developed by selection, as hitherto believed, and it is not necessary to insure discrimination by insectivorous vertebrates. The term, moreover, covers only certain classes of conspicuousness, while the term "immunity coloration" covers all cases of conspicuousness not attributable to selection. Immunity coloration includes on the one hand the conspicuous color characters of coral-reef fish where it has as its conditioning feature *inaccessibility;* it includes also the conspicuous color-characters of those insects which are, for one reason or another, unsuitable as food for vertebrate foes, and here it has as its conditioning feature *unpalatability* (whether due to stings, pricking hairs, disagreeable juices from the body cavity or glands, hard outer covering, etc.). It probably includes cases of so-called warning coloration among invertebrates other than insects (*e. g.,* Cœlenterata, nettling nudibranchs; see Hargitt, 1904) as well as among vertebrates. That immunity coloration may exist without the screen of unpalatability is shown by the following instances:

(*a*) According to Poulton (1887):

> Wallace has shown that the shape and colors due to sexual selection run riot in localities (certain islands) where enemies are largely excluded by barriers, and in the same way the brilliant colors of nauseous or dangerous insects may perhaps be explained by equal immunity, although due to other causes.

The work of Mayer (1900) throws serious doubt on the inference that colors such as those that have here run riot are sexual colors in the sense that they have a sexual function, and the whole condition is probably the result of immunity. According to Packard (1904) butterflies are not commonly eaten by birds. Their conspicuousness may therefore be wholly due to immunity.

(*b*) Marshall and Poulton (1902) make the following statement and illustrate it by instances:

> Swift-flying butterflies are not likely to be caught by birds. The latter learn the futility of pursuit. The butterflies have therefore been able to acquire brilliant colors above, particularly those species having protectively-colored undersides.

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(*c*) Saville-Kent (1893) describes three species of a huge anemone of the genus *Discosoma,* which occur on the barrier reef of Australia. One of these species "not infrequently measures as much as 2 feet in diameter." In the gastral cavity of each species of these anemones is commonly found a small fish of the genus *Amphiprion.* The three species of *Amphiprion* are all most conspicuously banded with orange-vermilion and white, but they differ in the number of white bands and in the fact that one of them, *A. percula,* has the white and vermilion bands everywhere separated by narrower black bars. Saville-Kent suggests that—

> The brilliant colors of the commensal guests attract the notice of other predatory fish, which, hastening to seize an apparently easy prey, are themselves entrapped within the outspread tentacles of the passively expectant sea-anemones.

(*d*) Belt (1874, pp. 196-197) says:

> Three gaudy macaws were wheeling round and round in playful flight, now showing all the red on the under surface, then turning all together, as if they were one body, and showing the gorgeous blue, yellow and red of the upper side gleaming in the sunshine; screaming meanwhile as they flew with harsh, discordant cries. This gaudy-colored and noisy bird seems to proclaim aloud that it fears no foe. Its formidable beak protects it from every danger, for no hawk or predatory mammal dares attack a bird so strongly armed. Here the necessity for concealment does not exist, and sexual selection has had no check in developing the brightest and most conspicuous colors. If such a bird was not able to defend itself from all foes, its loud cries would attract them; its bright colors direct them to its own destruction. The white cockatoo of Australia is a similar instance. It is equally conspicuous amongst the dark-green foliage by its pure white color, and equally its loud screams proclaim from afar its resting-place, whilst its powerful beak protects it from all enemies excepting man. In the smaller species of parrots the beak is not sufficiently strong to protect them from their enemies, and most of them are colored green, which makes them very difficult to distinguish amongst the leaves. I have been looking for several minutes at a tree, in which were scores of small green parrots, making an incessant noise, without being able to distinguish one; and I recollect once in Australia firing at what I thought was a solitary "green leek" parrot amongst a bunch of leaves, and to my astonishment five "green leeks" fell to the ground, the whole bunch of apparent leaves having been composed of them.

Newton (1893–1896) says of the macaw, of which there are about a score of species: "Their food . . . consists of various kinds of fruit . . . The sexes appear in all cases to be alike in colouring." We can, then, hardly attribute their colors to sexual selection. The food precludes aggressive resemblance. Belt's account makes it clear that we are not dealing with protective resemblance. Leunis (1883) says of the Psittaci: "Das Fleisch vieler arten gilt für zart und wohl-schmeckend," so that warning coloration on this score seems to be also precluded.

(*e*) Brown (1903, page 297, footnote), writing of the garter snakes of the moist region from latitude 40° in northern California to British Columbia, says:

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The liberty to indulge in the striking colors developed in the garter snakes of this region is partly due to the protection afforded by abundant vegetation, and perhaps in some degree to the absence of the three snake-eating genera, *Spilotes, Ophibolus,* and *Elaps.*

All these classes of cases may be brought under the head of immunity coloration and may be attributed to inaccessibility. There are doubtless many other similar cases to be found in the literature and many cases of conspicuousness in insects now attributed to unpalatability may be due to other conditions. That other circumstances than unpalatability and inaccessibility may condition immunity coloration is probable.

Immunity coloration may now be defined as "*coloration, not sexually dimorphic, which renders an organism in its natural environment conspicuous to vertebrates; which has no selective value, since it does not aid the organism in escaping vertebrate enemies by concealment (protective coloration), nor in approaching its accustomed invertebrate prey (aggressive coloration), and when associated with disagreeable qualities is unnecessary as a warning to vertebrate foes of the existence of such qualities (warning coloration); it is conceived to have arisen through internal forces under immunity of the organism from the action of selection on its color characters.*" The exclusion of all sexually dimorphic coloration from the definition is provisional.

The obvious relation usually observable between completed animal characters and their function or utility is reflected in the curious anthropomorphic feature of those modern theories of evolution that are founded on a relation between the evolution of these structures and utility. This viewpoint finds interesting expression in theories of animal coloration. Sexual coloration, warning coloration, and possibly recognition marks may have obvious, though perhaps not necessary, uses; their evolution is therefore assumed to have taken place in relation to these uses. The utmost ingenuity has been exercised to discover plausible utility in every fleck of color with the conviction that thereby *evidence* was being accumulated as to a mode of evolution. The theory of orthogenesis alone is free from this limitation, since it holds that characters may arise and be without utility or their utility be determined afterward. The present paper holds that immunity coloration has developed in no relation to utility, but it does not discuss the method of that development. The view is presented as a working hypothesis which it is hoped soon to further test.

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XI. SUMMARY.

This paper embodies a search for the biological significance of the conspicuousness which it attempts to show characterizes many of the coral-reef fish of the Tortugas region. After showing that this conspicuousness is not a secondary sexual character and that it serves neither for protective or aggressive resemblance its value as a warning character is subjected to experimental test.

Experimental evidence is presented to show that the gray snapper, the commonest predaceous fish of the region, discriminates certain colors, forms associations with great rapidity, and retains these associations for a considerable time (memory). If any of the coral-reef fishes possess a combination of conspicuousness with such unpleasant attributes as render them unpalatable, the gray snapper should have learned to avoid them at sight and their conspicuousness would then have a warning significance. It is shown that when atherina, an inconspicuous fish which serves normally as the food of the gray snapper, is given an artificial warning color and at the same time rendered unpalatable, it is, after a brief experience, no longer taken as food by the gray snapper. Artificially colored atherinas thus come to have a warning significance for the gray snapper and are avoided, even when not unpalatable, although normal atherinas are still readily eaten. The conclusion is thus reached that the existence of a warning coloration or of warning conspicuousness in coral fishes is easily possible.

This possibility was tested by feeding to gray snappers in their natural environment but at a distance from the reefs, conspicuous coral-reef fishes both living and dead. Of the 21 species thus fed all were taken by the gray snapper, with the exception of one which escaped by reason of the large size of the individual used. It is concluded that these coral-reef fishes do not possess that combination of conspicuousness with unpleasant attributes necessary to the theory of warning coloration. Their conspicuousness has no warning significance. Certain further evidence is presented to show that the rapidity and nicety of adjustment of the gray snapper to its food is such that it learns to avoid what is unpalatable without the necessity of its being warningly colored or otherwise conspicuous.

The conclusion is reached that the conspicuousness of coral-reef fishes, since it is not a secondary sexual character and has no necessary meaning for protection, aggression, or as warning, is without biological significance. The coral-reef fishes have no need of aggressive inconspicuousness because their food consists of invertebrates, chiefly fixed. They have no need of protective inconspicuousness because the reefs and their agility afford them abundant protection. Selection has therefore not acted on their colors or other conspicuous characters, but these have developed in the absence of selection and through internal forces. They are the result of race tendency, unchecked by selection.

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An attempt is made to apply this conclusion to the " warning coloration " of conspicuous insects. Evidence is collated to show that vertebrate foes are able to discriminate between palatable and unpalatable insects without the aid of a distinguishing conspicuousness. If such power of discrimination exists, then since unpalatability must have preceded conspicuousness in insects, this conspicuousness can not have been initiated by selection. If it began without the aid of selection it may well have continued to develop without it. The conspicuousness of warningly colored insects is then attributed to the avoidance of them by vertebrate foes at a time when they were still relatively inconspicuous. This avoidance rendered protective inconspicuousness unnecessary to them, while the nature of their food rendered aggressive inconspicuousness unnecessary. Their unpleasant attributes have protected them from their enemies, as the reefs have protected the coral-reef fish. Under this immunity from selection they have been free to develop conspicuousness, which is therefore regarded as an expression of race tendency, of internal forces, in the absence of selection.

The theory of *immunity coloration* is proposed as a substitute for the theory of warning coloration and it is shown that it covers certain cases not covered by the theory of warning coloration. Immunity coloration is defined on page 316.

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EXPLANATION OF PLATES.

[All figures are reproductions of instantaneous photographs made in the natural environment with a submerged camera on orthochromatic plates with the aid of a color screen.]

PLATE 1.

FIG. 1. Rock ledges near the beach, showing 3 *Abudefduf marginatus* banded with black and yellow-white, and 2 grunts (*Hæmulon* sp., apparently *sciurus*) striped with blue and yellow. A spherical "head" of living coral (*Porites*) in the middle background. Note the upper *Abudefduf* swimming by the use of the pectorals. When these fish are seen endwise against the surface film the bands blend and the fish are then almost invisible.

FIG. 2. *Abudefduf marginatus* seen in crevasses of a reef of massive coral. Note everywhere over the reef the mantle of living coral polyps (*Orbicella*).

PLATE 2.

FIG. 3. At least three *Hæmulon flavolineatum*, French grunt, among coral rocks and *Millepora* at the base of a reef. The stripes are silvery lavender-blue and chrome yellow. At the right a large snapper (apparently *Lutianus apodus*) conspicuously banded in black or brown and yellow.

FIG. 4. A small labroid fish of an unidentified species feeding on the rock bottom; at its left a branching gorgonian (*Plexaura*).

PLATE 3.

FIG. 5. Two blue surgeons (*Hepatus cæreuleus*) in front of a branching gorgonian (*Plexaura*) on bottom rock. Note the lancet in the caudal peduncle of the one at the right. In front of the surgeons a *Chætodon ocellatus*, the tail of which moved during exposure. The entire dorsal, anal, pelvics and caudal peduncle are spectral yellow.

FIG. 6. A *Chætodon capistratus* over an incrusting coral (*Mæandrina*) on bottom rock and in front of large gorgonian on which expanded polyps may be seen immediately over the fish. The fish is nearly gray, with much yellow on snout and fins.

PLATE 4.

FIG. 7. In the foreground *Iridio bivittatus* (slippery Dick) feeding on bottom. The stripes at a little distance appear black and white. In the background a second *Iridio bivitattus* above, and a *Hæmulon flavolineatum* or French grunt below.

FIG. 8. Massive coral (*Orbicella*) on the outer face of a reef. In the lower right-hand corner an *Elacatinus oceanops* clinging to the coral. The stripes are very light and very dark blue and appear nearly black and white. At the left an expanded tube-inhabiting annelid (*Spirobranchus tricornis*).

FIG. 9. The gray snapper (*Lutianus griseus*), as it appears over the coral sand near the shore; an instance of aggressive resemblance.

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PLATE 5.

FIG. 10. A group of large coral-reef fishes over a rock cleft in front of branching gorgonians. At the left two surgeons (*Hepatus hepatus*). The lancet is visible in the one at the right. A third surgeon at right of middle below also shows the lancet. These fish are practically black. In the center a French grunt (*Hæmulon flavolineatum*), striped with yellow and blue. At the left of this a blue parrot-fish (*Callyodon cæruleus*); at its right a green parrot-fish (probably *Callyodon vetula*). Beneath the green parrot-fish a mottled parrot (*Sparisoma?*). Above the grunt a second mottled parrot and to the left of this a third. Behind the green parrot a purple sea-fan (*Rhipidogorgia*). Note the position of the pectoral in the parrots and the left-hand surgeon.

FIG. 11. A group of large coral-reef fish, chiefly yellow and blue grunts, mostly *Hæmulon sciurus*. Among these at the left one or two gray snappers (*Lutianus griseus*). At the right are purple sea-fans (*Rhipidogorgia*) and to the left of these two large parrot fish. In front of the lower parrot fish a surgeon (*Hepatus hepatus*). A second surgeon farther to the left shows the characteristic mode of locomotion by the pectoral fins. This is seen also in the lower parrot. The camera was pointed toward the light, so that the markings of the fish are not as distinct as they would otherwise be.

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